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HOST EFFECTS ON THE POPULATION GENETICS AND DYNAMICS OF THE MOUNTAIN PINE BEETLE, *Dendroctonus ponderosae* HOPKINS (COLEOPTERA: SCOLYTIDAE)

BY

DAVID WILLIAM LANGOR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

SPRING 1989

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled HOST EFFECTS ON THE POPULATION GENETICS AND DYNAMICS OF THE MOUNTAIN PINE BEETLE, *Dendroctonus ponderosae* HOPKINS (COLEOPTERA: SCOLYTIDAE) submitted by DAVID WILLIAM LANGOR in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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DEDICATION

I dedicate this thesis to my parents, Fredrick and Emily Langor for their constant support, encouragement and love

ABSTRACT

The effect of lodgepole pine (LPP) and limber pine (LMP) on allozyme and morphological variation as well as population dynamics was investigated for epidemic and declining populations of the mountain pine beetle (MPB) in Alberta and eastern British Columbia. Although host effects were evident there was no evidence of host race formation.

Allozyme variation at five polymorphic and nine monomorphic loci was assayed for eight MPB populations in LMP and LPP. There were no significant host effects on heterozygosity. Genetic differentiation of beetles occurred among sites, individual conspecific trees within a site, generations, and sexes. Significant host effects on genetic differentiation occurred at three polymorphic loci at the White Pine Coulee site but not at the Jim Creek site. The host associated differentiation observed at the White Pine Coulee site is most likely attributable to differential survival of beetle genotypes among hosts rather than to differential host preference. Standardized discriminant function analysis of 12 morphological characters indicated significant sexual, geographical and host effects on beetle shape.

Populations of MPB from LPP and LMP were cross-bred with respect to host species. Host effects were evident for reproductive success, egg gallery length, number of eggs per

cm of gallery and fecundity of parents as well as development, mortality, dry weight and fat content of their progeny. Nonetheless, beetles reared from LPP and LMP were compatible with either host. There was no apparent barrier to prevent beetles from the two host species from inter-breeding in the field. Progeny of all crosses were fertile.

In co-occurring MPB field populations in LMP and LPP, beetles emerged from LPP 7-8 days earlier than from LMP. Beetles had higher fecundity, produced more eggs per cm of gallery, and their progeny developed faster and survived better in LMP than in LPP. There was no apparent phenological or other barrier which might inhibit gene flow between MPB populations in LMP and LPP. Both field and laboratory studies indicate that LMP is a better host for mountain pine beetle reproduction, development and survival than LPP. Thus, beetle populations may be able to increase much more quickly in LMP, arguing for regular monitoring of these populations.

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LIST OF ABBREVIATIONS

Abbreviation	Description
AAT	aspartate aminotransferase
AGP	α-glycerol-3-phosphate dehydrogenase
EST	esterase
E50	a development index calculated as the number of days from the time that beetles were mated in the laboratory until 50% of the brood emerged
H_I	individual heterozygosity
H_l	locus heterozygosity
I	Nei's (1972) genetic identity
IDH	isocitrate dehydrogenase
LDH	lactate dehydrogenase
LMP	limber pine
LPP	lodgepole pine
MDH	malate dehydrogenase
ME	malic enzyme
MNR	menadione reductase
MPB	mountain pine beetle
MPI	mannose phosphate isomerase
PGI	phosphoglucose isomerase
PGM	phosphoglucomutase
SDFA	standardized discriminant function analysis
TO	tetrazolium oxidase

I. INTRODUCTION

Biology of the mountain pine beetle

Mountain pine beetles (MPB), *Dendroctonus ponderosae* Hopkins, emerge from the trees in which they developed and fly to new living trees or fresh, fallen host material from July to mid-August. The process by which the MPB (and other scolytids) select their hosts has spawned much controversy (D.L. Wood 1982) with one school advocating primary attraction to volatiles emanating from stressed trees (Gara *et al.* 1984) and another advocating random dispersal and indiscriminant landing on hosts which are subsequently accepted or rejected based on gustatory cues (Moeck *et al.* 1981). Regardless of the exact process of host selection, it remains that *D. ponderosae* prefers certain species over others and certain individuals of a species over others of the same species (Amman and Cole 1983).

Once a suitable host is located and the female starts to bore into it, she comes into contact with the defenses of the host. Primary resinosis occurs when beetles sever resin ducts causing exudation of large quantities of resin which may flush beetles from the tree (Amman and Cole 1983). In addition to the pure mechanical effect of the resin defense system, resin also contains compounds that are toxic or repellant to beetles (Smith 1972).

Secondary resinosis (or a hypersensitive reaction) is caused by a localized autolysis of parenchyma cells which produces a necrosis in advance of the fungi introduced by the beetles. Resinosis follows in which resin and phenolics are derived *in situ* from secretory cells in the necrotic area rather than in the resin ducts (Matson and Hain 1983; Raffa and Berryman 1983).

Upon exposure to host resins, female *D. ponderosae* release trans-verbenol which is synthesized from the tree monoterpene α-pinene (Borden *et al.* 1987). Trans-verbenol acts as a population aggregation pheromone which, when synergized with host monoterpenes such as myrcene or α-pinene, serves to direct the attack of large numbers of beetles (biased towards males) to a particular tree (Borden *et al.* 1987).

Males join females anywhere from an hour to two days after the female commences pheromone production. Mating occurs in the egg gallery (Reid 1958). Acoustic signals (stridulation) are an important part of courtship (Michael and Rudinsky 1972). After joining females, males produce another pheromone, exo-brevicomin, which is attractive at low concentrations but anti-aggregative at high concentrations (Borden 1984). Thus, it is believed that when large numbers of males arrive at a tree the high concentration of exo-brevicomin produced by them combined with the anti-aggregative effects of verbenone, produced by

feeding individuals of both sexes, serves to prevent further attack on that tree. Usually attacks then switch to nearby trees (Borden 1984). Several of the semiochemicals produced by *D. ponderosae* are chiral and research has indicated that bark beetles can distinguish between optical isomers of their pheromones (Lanier and Burkholder 1974; Birch *et al.* 1980). Since pheromones are, at least partially, synthesized from precursors that originate from the host tree, the ability to produce a pheromone may be determined by the chirality of the precursor in the host tree.

After she is joined by a male the female commences egg gallery construction, which is upward and parallel with the grain of the wood. Egg gallery length varies with factors such as tree species, female size, phloem thickness, and population density (Amman and Cole 1983). Gallery length may be 60 cm or more but generally varies between from 25 to 35 cm (Amman and Cole 1983).

Blue stain fungi (*Ceratocystis* spp.) are symbiotes of *D. ponderosae* and are introduced into the tree by the beetles during colonization (Whitney and Farris 1970). The fungus invades the phloem, and especially the sapwood, where it helps to reduce resin flow and disrupt the vascular system. This aids successful colonization of the trees by beetles.

Eggs are laid in niches along the sides of the egg gallery (Amman and Cole 1983). The number of eggs per gallery varies with gallery length and is influenced by the same factors that influence gallery length. The average number of eggs laid per cm of gallery is usually between 1.7 and 2.3 (Amman and Cole 1983). Eggs hatch after about ten days and larvae start to feed on the phloem. They excavate short feeding galleries at right angles to the egg gallery in which they develop through four instars. Overwintering occurs generally in the second instar (Amman and Cole 1983). Pupation occurs in the tree from late May to June and emergence occurs from July to mid-August, depending on latitude and altitude. In Canada, *D. ponderosae* is univoltine except at high altitudes where it takes two years to complete development (Reid 1962).

Like that of many insects, population levels of *D. ponderosae* are cyclic, alternating between endemic (beetles and damage are difficult to detect) and epidemic (beetles are abundant and cause serious damage to forests) (Cole and Amman 1980). Epidemic populations are always present in some part of the range of the MPB. However, in any given area outbreaks occur only every 20 to 40 years, depending upon stand location and tree growth rate (Roe and Amman 1970; Amman and Baker 1972). In Canada, outbreaks have been reported in one area or another of Alberta and British Columbia since 1910 (Powell 1969). The most recent outbreak

started in the early 1970's in Canada (Van Sickle 1985; Alberta Forestry, Lands and Wildlife 1986). Populations started to decline in Alberta around 1983 (Moody and Cerezke 1984) and in British Columbia around 1984 (Wood and Van Sickle 1986). Populations are now endemic throughout Alberta, however, there are still outbreak populations in parts of British Columbia (Wood *et al.* 1987). Two major causes of outbreaks have been postulated: (1) widespread physiological maturity and decreased vigor of trees (Shrimpton and Thomson 1981, 1983) and (2) weather, especially drought (Powell 1969; Thomson and Shrimpton 1984).

Throughout its range in western North America *D. ponderosae* attacks all native and many exotic pines and occasionally other conifers (Furniss and Schenk 1969; McCambridge 1975; Smith *et al.* 1981; S.L. Wood 1982). Under epidemic conditions any or all acceptable host species may be attacked in a given geographical region and host switching commonly occurs (Richmond 1933; S.L. Wood 1982). However, strong preference by the MPB for one host species, even when other acceptable species are available, may occur (Baker *et al.* 1971). In phytophagous insects, host preference has important genetic and evolutionary consequences (Futuyma and Peterson 1985).

Influence of plants on insect genetics and evolution

It has long been recognized that many phytophagous insect species feed on more than one plant species and often exhibit different characters (morphological, biological) on different hosts (Walsh 1864). Since Walsh's (1864) pioneer discovery of biological races the concepts of "host races" and "biotypes" have kindled intense controversy among ecologists and evolutionists (Dethier 1954; Diehl and Bush 1984; Futuyma and Peterson 1985). Regional pest management programs for economically important insect species require a full understanding of host effects on insect populations and the underlying genetic basis for host-associated population differentiation in order to develop control strategies that are effective for all crops (Diehl and Bush 1984). However, more recently it has been realized that host races or biotypes may also represent the very type of genetic variation that is the focus of some important questions about mechanisms of organic evolution, i.e. coevolution and sympatric speciation (Futuyma and Peterson 1985; Mitter *et al*. 1988; Pamilo 1988).

Resource-associated genetic variation between populations is generated by the disruptive forces of genetic drift and natural selection (Slatkin 1973). For phytophagous insects, one of the the main selective pressures stems from the biological characteristics of the host plants, in addition to abiotic effects and natural enemies. However,

the diversifying effects of these disruptive forces are negated by the homogenizing effects of gene flow. Population genetics models indicate that an exchange of only one individual per generation between two populations may be enough to keep them from diverging by genetic drift (Slatkin 1987). Therefore, inhibition of gene flow is a necessary prerequisite for population differentiation.

It is easy to understand how restriction of gene flow between allopatric populations of insects inhabiting different host plants could be maintained. There are numerous studies of allopatric host-associated differentiation, e.g. for *Drosophila* (Heed 1978), *Niloparvata* (Claridge *et al.* 1982), *Bathyplectes* (Salt and van den Bosch 1967), *Leptinotarsa* (Hsiao 1978), and *Dendroctonus* (Anderson *et al.* 1979; Stock *et al.* 1979; Stock and Amman 1980). However, in these cases, as in many others, the influence of host on genetic differentiation is confounded by geographical variation. The necessary test of host-associated genetic differentiation requires that population samples be taken from different plants that are sympatric or in very close proximity (Futuyma and Peterson 1985). Studies of sympatric host-associated genetic differentiation are few (Bush 1975; Phillips and Barnes 1975; Mitter and Futuyma 1979; Jaenike and Selander 1980; Guttman *et al.* 1981; Stock and Amman 1983; Sturgeon and Mitton 1986). However, these examples and others have

generated frequent postulations that the response to differences between hosts is a primary factor in speciation in some phytophagous insect lineages (Mitter and Futuyma 1979; Mitter *et al*. 1988).

Sympatric speciation via host race formation has been a controversial topic for several decades. Researchers such as Thorpe (1930), Bush (1975), and Tauber and Tauber (1977) argue strongly that sympatric speciation is a common occurrence. The principal theoretical treatment of sympatric speciation is Maynard-Smith's (1966) which has served as the conceptual foundation for several cases of putative sympatric speciation, e.g. in *Chrysopa* (Tauber and Tauber 1977) and *Rhagoletis* (Bush 1969). However, the conditions for truly sympatric speciation appear to be so stringent that many researchers, although not denying its possible occurrence, doubt that it is common (eg., Mayr 1970; Futuyma and Mayer 1980).

Sympatric speciation along host lines is most probable when certain conditions are met. If mating does not occur on the host plant, strong selection, independent population regulation on the two hosts, and close linkage between the loci governing mating preference and adaptation to the hosts are necessary for speciation (Felsenstein 1981). If mating does occur on the host plant, genetic differentiation between the incipient species requires either that there be strong selection against genes that find their way to the

'wrong' host, thereby favouring reinforcement of reproductive isolation, or else that the attraction of different genotypes to different hosts imposes a strong barrier to gene flow. This is most likely to occur if host attraction is governed by a single locus at which there is full dominance and full penetrance (i.e., genotypes are not ambivalent or subject to frequent mistakes in host selection) (Maynard-Smith 1966; Dickinson and Antonovics 1973).

In contrast to the above stringent conditions required for sympatric speciation, both selection models (Templeton 1980; Lande 1981) and neutral models (Nei *et al.* 1983) find that speciation is readily achieved if there is some degree of spatial segregation. There is abundant empirical evidence for geographical (allopatric) speciation (Mayr 1970).

The existing data on host-associated variation within populations provide only meager support for the existence of conditions that would favour sympatric speciation. There is little evidence of fidelity to host as a result of larval conditioning (Claridge and Wilson 1978; Fox and Morrow 1981; Tabashnik *et al.* 1981). There are only a few cases of genetic differentiation among samples taken from different hosts in sympatry, and even fewer in which divergent traits are correlated with host preference. Additionally, there are no good examples of linkage disequilibrium between loci affecting preference and fitness (Thompson 1988).

Appreciable fitness differences among sympatric host-associated genotypes have been reported for a few sexual populations (Gallun 1977; Via 1984), but most cases of variation in fitness are in parthenogenetic forms (in which linkage disequilibrium among polygenes is more readily achieved) or between allopatric populations (in which linkage disequilibrium between genes governing adaptation and preference is not an issue) (Futuyma and Peterson 1985).

Perhaps the case which comes closest to fulfilling the criteria for sympatric speciation is the *Enchenopa binotata* Say complex of tree hoppers, in which the species differ in reproductive phenology, generally have lower fitness on each other's hosts, and mate only on their host plants (Wood 1980; Wood and Guttman 1983). However, even in this case the mode of inheritance of the traits is unknown and species have a very localized dispersal so that spatial isolation in the past cannot be ruled out.

On the basis of both theory and evidence it is more reasonable to favour, *a priori*, allopatric explanations over sympatric explanations in accounting for any given speciation event. It seems prudent to consider the possibility of sympatric speciation only on a case by case basis and to seek examples that more plausibly fit a sympatric than allopatric model (Futuyma and Peterson 1985). The MPB is a good study system because it reputedly exhibits host preference (Evenden *et al.* 1943; Baker *et al.* 1971) and

there are host effects on many life history parameters (Amman 1982).

Host-associated variation in the mountain pine beetle

The MPB has been the subject of hundreds of studies. Not surprisingly there are many records of host effects on various aspects of *D. ponderosae* biology, e.g. population dynamics and phenology (Billings and Gara 1975; Amman 1982; Safranyik and Linton 1982), chemical communication (McKnight 1979; Libbey *et al.* 1985), morphology and allozyme variation (Sturgeon and Mitton 1986). However, the host-associated differences reported in most of these studies occurred among allopatric populations.

During a recent (1975-1986) outbreak in Alberta, *D. ponderosae* infested lodgepole pine (LPP), *Pinus contorta* Douglas var. *latifolia* Engelmann and limber pine (LMP), *Pinus flexilis* James, which often occur in mixed stands (Alberta Forestry, Lands and Wildlife 1986). In 1985, I set out to determine if host preference is resulting in genetic differentiation of local MPB populations in LPP and LMP and if such genetic variation is correlated with differences in beetle morphology, population dynamics, and fertility and fecundity when cross-bred.

In Chapter II, I examine allozyme and morphological variation in field populations of *D. ponderosae* and compare these traits among localities, years, sexes, individual

conspecific trees within a locality, and host species. The principal objective of this investigation was to assess whether the breeding structure of the MPB populations in Alberta was sub-divided along host lines.

In Chapter III, I report on controlled breeding studies designed to investigate the possibility of reproductive isolation among *D. ponderosae* from LPP and LMP. Relative compatibility and fecundity of beetles cross-bred with respect to juvenile host was measured along with development, mortality and fertility of their progeny.

In Chapter IV, I assess phenological differences among *D. ponderosae* field populations associated with LPP and LMP to determine if observed differences could provide a barrier to gene flow between populations. Additionally, this study compares the relative suitability of LPP and LMP for *D. ponderosae* reproduction, development, and survival in the field.

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II. ALLOZYME AND MORPHOLOGICAL VARIATION

A. Introduction

Genetic variation and its spatial/temporal structure and dynamics are central to evolutionary theory (Nevo 1978). With the application of electrophoretic techniques to studies of genetic variation in recent years, much attention and controversy have been focused on the role of environmental heterogeneity in maintaining genetic diversity within and among natural populations (Hedrick *et al.* 1976; Nevo 1976,1978; MacKay 1981; Via and Lande 1985). In addition to abiotic effects and natural enemies, one of the most important environmental variables influencing phytophagous insects is the host plant (Diehl and Bush 1984; Futuyma and Peterson 1985), and genetic differentiation has been associated with host plant use in several phytophagous species (Edmunds and Alstad 1978; Mitter and Futuyma 1979; Jaenike and Selander 1980; Guttman *et al.* 1981; Stock and Amman 1983; Sturgeon and Mitton 1986a).

In western North America the MPB is a serious pest of most native pine species within its range (Safranyik *et al.* 1981; Amman and Cole 1983). The MPB completes development in the phloem/cambium layer of the tree by mid-summer and adults disperse to new trees (selected by females) where mating and oviposition occurs (Amman and

Cole 1983). In the foothills of Alberta *D. ponderosae* infests LPP and LMP, which often occur in mixed stands (Alberta Forestry, Lands and Wildlife 1986). Also, some whitebark pine stands, *Pinus albicaulis* Engelmann, are infested by *D. ponderosae* at high elevations in the Rocky Mountains.

In this study I compare allozyme and morphological variation of field populations of *D. ponderosae* in Alberta and British Columbia among localities, years, sexes, individual conspecific plants within a locality, and host species. As part of an overall study of host effects on the population genetics and dynamics of *D. ponderosae*, the principal objective of this investigation was to assess whether the breeding structure of MPB populations in Alberta was subdivided among host species. If so it is expected that allozyme and morphological variation of *D. ponderosae* would reflect differences in host plant use. Since this is the only study of allozyme variation in Canadian populations of *D. ponderosae* occurring at the northern limits of its range on the east slopes of the Rocky Mountains, it also provides an interesting comparison to similar studies of more southern MPB populations in the United States (Stock and Guenther 1979; Higby and Stock 1982; Stock and Amman 1983; Stock *et al.* 1984; Sturgeon and Mitton 1986a).

B. Materials and Methods

Enzyme variation

Study sites and beetle collection. From 1985-87 adult *D. ponderosae* were collected from three host species at eight sites in southwestern Alberta and eastern British Columbia (Table II-1, Fig. II-1). Forest composition was similar at the White Pine Coulee, Jim Creek, Skyline Road, Snake Road, and Muddypound Creek sites (in the Porcupine Hills) (Table II-1). However, LMP was lacking at the Yarrow Creek, Palliser River and Sage Mountain sites located in the mountains. The Sage Mountain site was higher in elevation (at about 1800 m) than the other seven sites (at 800-1200 m). All *D. ponderosae* populations sampled were in the declining or endemic phase of their population cycle except for the Palliser River population which was epidemic (Table II-1). Beetle-infested LPP and LMP were in close proximity at only two sites, White Pine Coulee and Jim Creek, and even at those sites infested LPP and LMP were separated by approximately 400 m. Generally, infested LMP stands were about 100-150 m higher in altitude than infested LPP stands.

More than 2000 beetles were sampled from the eight localities. Most adults were collected in July of each year, just prior to emergence from their hosts. Mortality

of immature stages within the trees was estimated at 90-99% for the seven declining and endemic *D. ponderosae* populations and 75-85% for the epidemic Palliser River population (unpublished data). Dead, infested trees were debarked and beetles were collected from as many egg galleries and trees as possible in order to obtain a good cross section of the genetic variability at each locality. Collected beetles were placed in 10 cm diameter petri dishes, about 100 per dish, lined with moistened filter paper. Petri dishes were transported to the laboratory in a cooler and then were stored at 2-4 °C in sealed plastic bags. The filter paper in each dish was moistened and dead beetles were discarded every 4-5 days. In this manner beetles could be kept alive with < 10% mortality per month for two months. However, beetles were processed as quickly as possible and were seldom stored more than 6 weeks.

Beetles collected from some sites were sexed before electrophoresis using the method of Lyon (1958) or after electrophoresis by staining for lactate dehydrogenase [LDH (EC 1.1.1.27)] which exhibits sexual dimorphism in *D. ponderosae* (Sturgeon 1980). In 1985 at the White Pine Coulee and Jim Creek sites, beetles from individual trees were kept separate to provide a measure of genetic divergence among individual conspecific trees within a site. In other years and at other sites beetles from

different conspecific trees were pooled.

Populations of *D. ponderosae* from two sites (Jim Creek and Palliser River) were sampled twice in one generation - just prior to winter and again after winter to investigate the effects of overwintering on allele frequencies and heterozygosity. The *D. ponderosae* populations in LMP and LPP at Jim Creek were sampled in late August of 1985 and the population in LMP was sampled again in early July 1986 (no beetles in LPP survived the winter). The population in LPP at Palliser River was sampled in late August in 1986 and again in early July 1987. Sampling of the populations before winter involved cutting slabs from infested trees with a chainsaw and rearing the larvae and eggs to maturity in the laboratory. Adult beetles from the same trees were sampled again after winter in the manner outlined above.

Electrophoretic procedures. Beetles were placed individually into 0.5 ml beaker cups with 0.1 ml of extraction buffer (Yeh and O'Malley 1980). The cups and their contents were maintained in an ice water bath while beetles were being homogenized. Filter wicks (12 X 3 mm) were cut from Whatman no. 2 filter paper and immersed in the beetle homogenate, blotted briefly on tissue paper and loaded on to horizontal gels made from a 12.5% (wt./vol.) solution of hydrolyzed potato starch (Connaught Laboratories, Lot 431-1). Diluted food dye and

homogenate of corn ("Spancross" hybrid) were used as markers and references. The details of preparing, loading, running and slicing gels are well explained and illustrated in Conkle *et al.* (1982). Stain recipes were adapted from Shaw and Prasad (1970), Harris and Hopkinson (1976) and Conkle *et al.* (1982).

Four buffer systems, lithium-borate (Ridgeway *et al.* 1970), Histidine-EDTA (Namkoong *et al.* 1979), Tris-citrate (Siciliano and Shaw 1976) and Tris (Schaal and Anderson 1974) were used to screen 42 enzyme systems of which 11 (14 gene loci; 5 polymorphic and 9 monomorphic) produced consistently interpretable banding patterns and were selected for routine assay. They were esterase [EST (EC 3.1.1.1)], asparate aminotransferase [AAT (EC 2.6.1.1)], phosphoglucomutase [PGM (EC 5.4.2.2)], phosphoglucose isomerase [PGI (EC 5.3.1.9)], malic enzyme [ME (EC 1.1.1.40)], tetrazolium oxidase [TO (EC 1.15.1.1)], isocitrate dehydrogenase [IDH (EC 1.1.1.42)], mannose phosphate isomerase [MPI (EC 5.3.1.8)], menadione reductase [MNR (EC 1.6.99.2)], α-glycerol-3-phosphate dehydrogenase [AGP (EC 1.1.1.94)] and malate dehydrogenase [MDH (EC 1.1.1.37)]. Additionally, LDH was used to sex some beetles. In all cases, a migration distance of 5 cm in the anodal direction for the dye marker provided adequate resolution of banding patterns.

Data analysis. Electrophoretic data were analysed using the computer program BIOSYS-1 (Swofford and Selander 1981). Allele frequencies were calculated for all groups. Observed genotype frequencies were compared to values derived from random mating (Hardy-Weinberg) expectations. Nei's (1972) genetic identity (I) values were calculated using data from all loci. Chi-square contingency tests, based on the observed numbers of each allele at a single locus, were used to compare gene frequencies among sites, years, sexes and hosts. Because of low (< 5) numbers of several alleles in many groups of beetles, data for those alleles were combined with data for alleles with the next closest Rf values for statistical analysis. The alleles for which data were combined were: alleles 0,1 and 2 of EST2; 5 and 6 of EST2; 0 and 1 of AAT1; 2 and 3 of AAT1; 0 and 1 of PGM; 2 and 3 of PGM; 1 and 2 of PGI; 3 and 4 of PGI.

Two heterozygosity measures were calculated:
(1) Locus heterozygosity (H_L) was used for interpopulation comparisons of heterozygosity of individual polymorphic loci. H_L was calculated using the "direct-count" method, i.e. the proportion of individuals sampled that are heterozygous. Additionally, for each population H_L was averaged (simple arithmetic) over the five polymorphic loci as well as over all 14 loci.
(2) Individual heterozygosity (H_I) - An H_I score, the

proportion of the five polymorphic loci that were heterozygous, was calculated for each beetle for which all data were available. Individual H_I scores were subjected to log transformation [log X+1] and analyses of variance were used to compare H_I between sites, years, sexes and hosts.

Morphological variation

For morphometric analysis 140 beetles were collected from LPP and LMP at White Pine Coulee, LMP at Jim Creek and Skyline Road, and LPP at Yarrow Creek at the same time that beetles were collected for electrophoretic studies. These specimens were preserved in 70% ethanol until sexed and measured for 12 morphological characters: length of pronotum along the midline, maximum width of pronotum, distance between bases of antennae, distance between the eyes, eye length, eye width, elytra length, metepisternum length, distance between mesocoxae, length of pro-tibia and length of pro-femur.

Stepwise discriminant function analyses (SDFA) were used to compare males and females, beetles from different sites, and beetles inhabiting different host species and to identify the characters contributing most to the discrimination. For each successive step in the analyses, the variable that produced the largest increase in Rao's V (generalized measure of overall separation between

groups) was selected (Nie *et al.* 1975). Analyses of variance were used to compare each character individually among groups of beetles.

C. Results

Allozyme variation

Significant deviations of genotype frequencies from Hardy-Weinberg expectations were observed at all polymorphic loci and for at least one locus in all beetle groups except groups 12 and 16 and for as many as three loci in six groups (2, 4, 6, 11, 14, and 15) (Table II-2). Thirteen of the 16 groups exhibited significant deviations at the ME locus and all were attributed to heterozygote deficiencies. However, only three of the 16 deviations observed at the other four polymorphic loci were attributed to heterozygote deficiencies.

Locus heterozygosity (H_L) varied between sites, hosts, years and time of year (Table II-2). H_L averaged over all 14 loci varied from 10-13% and H_L averaged over the five polymorphic loci averaged from 27-36% (Table II-2). There was no significant host-associated difference in H_L values among populations.

Beetles from different sites were not well differentiated (all loci considered) since coefficients of identity (I) (Nei 1972) all exceeded 0.978 (Table

II-3). However, when polymorphic loci were analysed individually, allele frequencies of beetles from different sites differed at four loci (Table II-4). There was generally little differentiation among years (=generations) for beetle populations at a given site (Table II-5). Of 20 χ^2 tests (4 sites x 5 polymorphic loci) only four were significant (Table II-5). Overall, H_I did not differ between sites (Table II-4) or years within a site (Table II-5).

Seven of the 16 groups of beetles were sexed. Coefficients of identity comparing sexes of each group all exceeded 0.995 (Table II-6). When polymorphic loci were analysed individually only four significant differences occurred out of 35 comparisons (Table II-6). Of the seven groups of beetles only one (group 4) exhibited a difference in H_I between sexes (Table II-6) with males having a lower H_I value.

A single generation of beetles was sampled before and after winter at two sites: Palliser River (groups 6 and 7) and Jim Creek (groups 10 and 11). Although I > 0.99 for both populations, when polymorphic loci were analysed individually beetles collected before and after winter at Jim Creek differed at the PGM locus and those collected at Palliser River differed at loci coding for EST2, AAT1, PGM, and ME (Table II-7). For MPB populations in LMP at Jim Creek, the frequency of allele 1 of PGM

increased and that of allele 2 decreased over the winter. The opposite effect occurred among populations in LPP at Palliser River where the frequency of allele 1 decreased and that of allele 2 increased. There were no significant differences in H_I among sampling dates for either population (Table II-7).

For three groups (1, 8 and 9) data from beetles collected from individual conspecific trees within a site were kept separate to provide a measure of inter-tree variation in beetle allele frequencies and H_I. Although I = 0.999 for each of the three beetle groups (Table II-8), individual analysis of polymorphic loci revealed that there was significant differentiation at the PGI locus among LPP trees as well as at EST2 and ME among LMP at White Pine Coulee (Table II-8). Additionally, EST2, AAT1 and PGM differed among LMP trees at Jim Creek. There were no differences in H_I between trees at either site (Table II-8).

The White Pine Coulee (groups 1 and 8) and Jim Creek (groups 3,10) sites were most useful for making comparisons among beetles from different host species since infested LPP and LMP occurred in close proximity at both sites thus minimizing geographical effects. Within each site beetles from different host species were almost identical genetically (I = 0.999) (Table II-9). At White Pine Coulee, where beetles were collected from both hosts

in early July, there was significant differentiation at three of the polymorphic loci (Table II-9). At Jim Creek, where beetles were collected before winter and reared in the laboratory, there was no differentiation. At White Pine Coulee, beetles from LMP were significantly more heterozygous than those from LPP but there was no difference in H_I among beetles from LPP and LMP at Jim Creek (Table II-9).

Morphological variation

Male and female *D. ponderosae* differ significantly ($\chi^2 = 182.5$, $p < 0.001$) in shape as indicated by SDFA involving seven of the 12 morphological characters (Table II-10). Also, analysis of variance demonstrated that females were significantly larger than males for 11 of the 12 characters (Table II-11).

The SDFA of shape variation of beetles among the four collection sites utilized nine characters (Table II-12). The first discriminant function was highly significant ($\chi^2 = 87.1$, $p < 0.001$), the second moderately significant ($\chi^2 = 27.6$, $p = 0.035$) and the third was not significant ($\chi^2 = 8.6$, $p = 0.28$). Only eye length and the distance between the meso-coxae were significantly different among beetles from different sites (Table II-11).

Host effects on beetle morphology were considered using only the subset of beetles from White Pine Coulee where LMP and LPP infested by *D. ponderosae* occurred in close proximity. Although the SDFA (Table II-13) detected significant host effects on overall beetle shape (χ^2 = 24.8, p = 0.006), when each character was examined individually using analysis of variance there were no host effects (Table II-11). Overall, differences among beetles from different sites were greater than differences among beetles from different hosts within a site.

D. Discussion

Allozyme variation

Although significant deviations of genotype frequencies from expectations based on Hardy-Weinberg equilibrium were detected at all loci, the most striking pattern was detected at the ME locus where 13 of the 16 beetle groups exhibited significant deviations from the expected (Table II-2). All of the deviations at the ME locus were attributed to heterozygote deficiencies, whereas only three of the 16 deviations detected at the other four polymorphic loci were attributed to heterozygote deficiencies. Differences in allele frequencies between males and females cannot account for the heterozygote deficiencies observed in this study

since there was little effect of sex on allele frequencies (Table II-6). Sex-linkage was ruled out because heterozygotes occurred in both sexes. Emergence of heterozygous and homozygous beetles at different times (Florence and Kulhavy 1981) might affect genotype frequencies, but in this study beetles were collected from the trees before emergence. Sturgeon and Mitton (1986a) argue that the heterozygote deficiencies they observed within *D. ponderosae* populations may be explained by the Wahlund effect, i.e. apparent panmictic populations of beetles were in fact composed of several sub-populations (divided along host lines) between which breeding was restricted. This explanation is untenable for populations studied in Alberta because heterozygote deficiencies at the ME locus were also detected among beetles from the same host species at a site (Table II-2) as well as among beetles within individual trees. Inbreeding is also an unlikely cause of heterozygote deficiencies since it would affect all loci. There were only three cases of heterozygote deficiencies at the other four loci. It is possible, but unlikely, that assortive mating may be linked to the ME locus. It is also possible that a null allele may result in heterozygote deficiencies. Null alleles have not yet been discovered at the ME locus in insects. It therefore seems that the most likely explanation for deficiencies of heterozygotes is that they are at a selective

disadvantage in both host species studied here.

Individual heterozygosity (H_I) is useful for comparing heterozygosity of individual beetles among populations. There were no significant geographical, temporal, sex or host effects on (H_I) of beetles sampled in this study (Tables II-4 to II-9) although Sturgeon and Mitton (1986a) found *D. ponderosae* from LMP to be significantly less heterozygous than beetles from either LPP or ponderosa pine in Colorado.

Locus heterozygosity (H_L) is useful for comparing allelic structure of individual loci among populations. Again, there were no clear trends among the H_L data (Table II-2). Average H_L (all loci considered) ranged from 10.0-11.2% for LPP beetles, 10.6-12.9% for LMP beetles and was 9.6% for the one population of beetles from whitebark pine (Table II-2). H_L values ranging from 9.6-17.0% have been reported for *D. ponderosae* populations in the United States (Stock and Amman 1980, 1983; Higby and Stock 1982; Stock *et al.* 1984). However, the usefulness of making comparisons of average H_L between studies is questionable since different researchers usually assay different loci as well as different proportions of polymorphic and monomorphic loci. Comparisons of H_L of the same locus between studies would be more meaningful but H_L data for individual loci have not been published in other studies of *D. ponderosae*

allozyme variation.

D. ponderosae populations in Alberta and eastern British Columbia are quite heterogeneous as indicated by significant genetic differentiation at four of five polymorphic loci (Table II-4). However, gene frequencies changed very little from year to year at a given site (Table II-5). Perhaps this indicates that there is little long range dispersal of beetles between sites.

Comparisons of groups of *D. ponderosae* using Nei's (1972) genetic identity yielded I values ranging from 0.979 to 0.999 (Tables II-3, II-5 to II-9), which are typical for different conspecific populations of invertebrates (Ayala *et al.* 1974), vertebrates (Selander and Johnson 1973) and plants (Gottlieb 1977). Although genetic similarity measures have proved useful for comparing genetic divergence between species and higher taxa, they generally are too insensitive to be useful when comparing subspecific taxa (Avise 1974). For such lower taxa, comparisons of allele frequencies of individual polymorphic loci among groups yield more interesting and useful information.

Over the past decade electrophoresis has been widely used to study allozyme variation in most species of *Dendroctonus*. Early studies documented significant genetic differences thought to be associated with

utilization of different host species or sub-species for *Dendroctonus pseudotsugae* Hopkins (Stock *et al.* 1979), *D. frontalis* Zimmermann (Anderson *et al.* 1979; Namkoong *et al.* 1979) and *D. ponderosae* (Stock *et al.* 1978; Stock and Amman 1980). Although host tree species was implicated in maintaining genetic heterogeneity among populations of beetles in each of these studies, these conclusions are questionable since beetles from the different host species were not sampled at the same site. Thus, genetic variation associated with host use may have been confounded with geographical variation.

This study was designed to determine the effects of host species (LPP and LMP) on genetic (allozyme) variation within localized populations of *D. ponderosae*. At the White Pine Coulee site significant differentiation among beetles from LMP and LPP was detected at three of five polymorphic loci (Table II-9). The differentiation at the esterase locus (EST2) is especially interesting since esterases have been implicated in insect detoxification systems (Krisch 1971). Esterases are among the most variable enzymes known and it is believed that their high levels of polymorphism probably reflect variation in food substrates available to the organism (Gillespie and Kojima 1968). Esterase loci consistently exhibit significant variation among beetles from different host species (Stock *et al.* 1978,1979; Namkoong

et al. 1979; Stock and Guenther 1979; Stock and Amman 1983; Sturgeon and Mitton 1986a).

In more recent studies of allozyme variation within *D. ponderosae* populations in the United States, Sturgeon and Mitton (1986a) detected significant differences among beetles from LMP, LPP and ponderosa pine at two of five polymorphic loci and Stock and Amman (1983) detected significant differentiation among beetles from LPP and ponderosa pine at two of six loci. In both of the previous studies and in this study, beetles that were sampled electrophoretically were collected from their hosts before emergence. Therefore, the observed genetic divergence among beetles from different host species could represent either (1) differential host preference, and thus subdivision of the breeding structure of *D. ponderosae* populations along host lines, (2) differential survival of beetle genotypes due to the selection pressures in each host, or (3) some combination of both. In future work, possible effects of differential selection pressures among host species could be eliminated by also collecting beetles during the host selection and colonization phase.

This study suggests that differential selection pressures mediated by the host have a greater effect on genetic differentiation of *D. ponderosae* than does preferential host selection. There was no genetic

differentiation among beetles from LPP and LMP at the Jim Creek site (Table II-9). Those beetles were reared from slabs cut from trees three weeks after they were attacked in the field. It is reasonable to expect that differences in selection pressures between LPP and LMP may not be as great in the slabs as in standing trees because the resin (likely one of the most important selective force affecting subcortical insects) was drained from the slabs and because differential mortality due to natural enemies could also be affected. By so reducing the differential selection pressures between LPP and LMP much more emphasis must be placed on host preference on the part of the beetles to explain any host associated genetic differentiation. It thus follows that the lack of such genetic differentiation among beetles from LPP and LMP at Jim Creek suggests that differential selection pressures among host species accounts for most of the host associated genetic differentiation of beetles at White Pine Coulee.

Additionally, beetles reared from slabs cut from infested trees in the field before winter (August) were genetically different from beetles collected from the same trees after winter (July) (Table II-7). Although only one of five polymorphic loci was significantly different among beetles collected from LMP at Jim Creek, four of five loci were significantly different among

beetles collected from LPP at the Palliser River site. The changes in allele frequencies of beetles among times of collection can only be explained as a consequence of the length of time that beetles were subjected to the selective environment of the trees; beetles collected from slabs before winter likely experienced reduced selective pressures compared to those remaining in the tree until the following July. The fact that the frequency of allele 1 of PGM increased and that of allele 2 decreased over the winter in LMP at Jim Creek while allele 1 decreased and allele 2 increased in frequency in LPP at Palliser River suggests possible differential selection pressures between host species. However, these effects could also be related to geographic variability. Mortality of beetles in slabs cut before winter was estimated at between 50% and 70%, whereas mortality of beetles remaining in the trees was between 80% and 95% (unpublished data). It is uncertain whether selective pressures were mediated by the chemical/physical environment of the trees or the winter climate (cold, dehydration), natural enemies or some combination of all.

Genetic differentiation also occurred among beetles from individual conspecific trees within a site (Table II-8). Since it is unlikely that aggregation could be genotype specific then genetic differentiation of beetles must be explained by the different selection pressures

among conspecific trees. Similar genetic differentiation among *D. ponderosae* from individual conspecific trees at a site was also reported by Sturgeon (1980). Considerable differences in chemical composition (especially monoterpenes) occur among conspecific pines (Squillace 1976; Smith 1977; Sturgeon and Mitton 1986b). If genetic differentiation can occur among beetles from conspecific trees then surely equal or greater levels of differentiation can occur among beetles inhabiting different species. The higher level of genetic differentiation of beetles among LMP as compared to LPP (Table II-8) suggests that LMP may be a more variable selective environment.

Thus, the genetic evidence lends little support to scenarios of host preference or fidelity by *D. ponderosae* in explaining the host effects on beetle allozyme variation in this study. In fact, there is very little evidence among scolytids in general to suggest that females prefer to oviposit in the same host species in which they were reared (Wood 1963). In Alberta, I have observed that *D. ponderosae* often colonizes only one host species consistently in an area where other hosts also occur. However, if this observation is to be used to argue in favour of host preference it must be assumed that the uninfested host species in that area is "available" for colonization. The uncolonized hosts may

simply be resistant to beetle attack (Cates and Alexander 1982). In many areas of the Alberta foothills we observed that although only one host species was infested by *D. ponderosae* many trees of the other species exhibited signs of unsuccessful attacks, i.e., pitch tubes. This suggests that *D. ponderosae* is attracted to and attacks all potential host species in an area but that sometimes one species is more resistant than the other.

Although allele frequencies were different for *D. ponderosae* from whitebark pine as compared to populations from LPP and LMP (Table II-2), any comparisons of host effects on the genome are confounded with geographical effects.

Morphological variation

Since substantial genetic change may not be detectable at early stages of differentiation (Lewontin 1974; Carson 1975), the allozyme data were supplemented with morphological data. Some subspecific taxa that are clearly defined morphologically and/or ecologically exhibit little genetic differentiation (Boller and Bush 1973; Avise 1974).

Due to the geographical effects on morphology (Table II-12) only beetles from White Pine Coulee were used to investigate host effects on beetle shape. Although no single character differed significantly among hosts

(Table II-11), a SDFA using 10 of the 12 characters (Table II-13) detected significant host effects on beetle shape. Sturgeon and Mitton (1986a) also reported significant host effects on overall shape of *D. ponderosae*. Four of the six characters (pronotal width, pronotal length, distance between the antennae, distance between the eyes) that they used to discriminate among beetles from different hosts were also used to discriminate among beetles from LPP and LMP in this study. The host effects on MPB morphology are complex. Clearly beetle shape is affected by host but it is not clear how important such effects are in comparison to differences between sexes (Table II-10) and among sites (Table II-12). An investigation of the effects of individual conspecific trees within a site on *D. ponderosae* morphology may help sort out these complexities.

Table II-1. Sites and host trees from which *D. ponderosae* were sampled electrophoretically.

Site (Code)	Coordinates	Host[1]	Year[2]	No. beetles	Forest composition	Population level
White Pine	49° 49' N	LPP	84/85	235 (4)[3]	LPP,LMP,DF,ES,ASP	declining
Coulee (WPC)	113° 55' W	LPP	85/86	199 (4)	"	endemic
		LMP	84/85	148 (5)	"	declining
Jim Creek (JC)	49° 48' N	LPP	85/86[4]	148 (4)	"	endemic
	113° 59' W	LMP	84/85	163 (5)	"	declining
		LMP	85/86[4]	132 (3)	"	endemic
		LMP	85/86	144 (3)	"	endemic
Yarrow Creek	49° 12' N	LPP	84/85	76 (8)	LPP,ES,DF	declining
(YC)	114° 2' W					
Skyline Road	49° 57' N	LMP	84/85	97 (10)	LPP,LMP,DF,ES,ASP	declining
(SR)	113° 59' W					

Table II-1 cont'd

Snake Road (SNR)	49° 39' N 114° 2' W	LMP	85/86	162 (15)	LMP,DF,ES,ASP	declining
Sage Mountain (SM)	49° 12' N 114° 10' W	WBP	85/86	33 (2)	LPP,WBP,WS,AF	declining
Muddy pound Creek (MP)	49° 53' N 113° 56' W	LMP	85/86	263 (22)	LPP,LMP,DF,ES,ASP	declining
		LMP	86/87	60 (2)	"	endemic
Palliser River (PR)	50° 32' N 115° 23' W	LPP	85/86	224 (14)	LPP,DF,ES	epidemic
		LPP	86/87'	192 (6)	"	epidemic
		LPP	86/87	86 (4)	"	epidemic

' LPP- lodgepole pine, LMP- limber pine, WBP- whitebark pine, DF- Douglas fir, ES- Engelmann spruce, ASP- trembling aspen, WS- white spruce, AF- alpine fir;

Table II-1 cont'd

[2] At each site adult beetles were collected from beneath the bark of trees in July of the latter year unless otherwise noted;

[3] numbers in parentheses represent numbers of trees from which beetles were sampled;

[4] beetles were reared from slabs cut from infested trees in late August and thus did not overwinter.

Table II-2. Allele frequencies, number of beetles sampled, χ^2 comparisons of observed to expected (Hardy-Weinberg) numbers of each genotype, and locus heterozygosity values (H_L) for mountain pine beetle populations in Alberta and British Columbia.

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Site	WPC	WPC	JC	YC	PR	PR	PR	WPC	JC	JC	JC	SR	SNR	MP	MP	SM
Year	84/85	85/86	85/86	84/85	85/86	86/87	86/87	84/85	84/85	85/86	85/86	84/85	85/86	85/86	86/87	85/86
Host	LPP	LPP	LPP	LPP	LPP	LPP	LPP	LMP	LMP	LMP	LMP	LMP	LMP	LMP	LMP	WBP
Locus/ Allele																
EST2																
0 (0.64)	0.002	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.007	0.000	0.000	0.000
1 (0.61)	0.019	0.015	0.014	0.007	0.024	0.000	0.017	0.014	0.021	0.019	0.038	0.037	0.022	0.012	0.010	0.016
2 (0.57)	0.447	0.444	0.371	0.386	0.420	0.326	0.414	0.368	0.448	0.427	0.376	0.511	0.391	0.400	0.390	0.422
3 (0.53)	0.313	0.283	0.354	0.382	0.276	0.376	0.345	0.338	0.344	0.373	0.285	0.271	0.308	0.360	0.370	0.219
4 (0.49)	0.121	0.133	0.129	0.105	0.129	0.154	0.121	0.118	0.055	0.092	0.183	0.106	0.163	0.081	0.120	0.063
5 (0.45)	0.085	0.117	0.102	0.105	0.137	0.128	0.095	0.139	0.126	0.077	0.118	0.074	0.105	0.135	0.100	0.281
6 (0.40)	0.013	0.005	0.031	0.013	0.015	0.017	0.009	0.024	0.006	0.004	0.000	0.000	0.004	0.012	0.010	0.000
N	235	196	147	76	205	149	58	148	163	130	93	94	138	211	50	32
χ^2	17.2	37.6*	17.2	79.0**	45.8**	20.5*	7.2	44.1**	22.3	22.0	6.9	9.2	17.6	42.1**	0.6	6.3
H_L	0.711	0.679	0.694	0.684	0.795	0.758	0.621	0.716	0.699	0.577	0.656	0.660	0.703	0.687	0.640	0.750
AAT1																
0 (0.72)	0.000	0.003	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.008	0.004	0.005	0.000	0.002	0.000	0.000
1 (0.66)	0.553	0.623	0.557	0.638	0.566	0.637	0.565	0.568	0.574	0.477	0.645	0.532	0.617	0.612	0.627	0.485
2 (0.57)	0.445	0.374	0.439	0.362	0.414	0.363	0.429	0.429	0.426	0.508	0.351	0.463	0.383	0.386	0.373	0.515
3 (0.50)	0.002	0.000	0.003	0.000	0.000	0.000	0.000	0.003	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000
N	235	195	148	76	220	190	85	148	163	131	138	95	158	259	59	33
χ^2	2.3	1.2	7.9*	3.9*	1.5	3.6	1.8	1.8	1.2	3.6	2.0	0.9	2.0	0.9	0.0	0.3
H_L	0.464	0.446	0.392	0.566	0.445	0.400	0.447	0.466	0.448	0.565	0.507	0.516	0.525	0.490	0.475	0.545

Table II-2 cont'd

PGM																
0 (0.94)	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.004	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1 (0.83)	0.101	0.121	0.130	0.091	0.136	0.268	0.153	0.203	0.199	0.156	0.246	0.147	0.410	0.189	0.339	0.034
2 (0.73)	0.897	0.876	0.870	0.909	0.859	0.732	0.847	0.793	0.794	0.844	0.754	0.853	0.590	0.811	0.661	0.966
3 (0.60)	0.003	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000
N	199	145	142	66	99	84	49	138	153	128	63	95	39	74	59	59
χ^2	0.8	17.1**	1.4	0.7	2.7	5.2*	1.1	4.0	4.6	0.3	6.7*	0.8	0.1	3.2	6.4*	0.0
H_L	0.196	0.159	0.204	0.182	0.283	0.298	0.224	0.319	0.314	0.250	0.492	0.274	0.513	0.243	0.305	0.069
PGI																
1 (1.90)	0.023	0.015	0.003	0.007	0.004	0.003	0.000	0.037	0.012	0.011	0.018	0.010	0.004	0.027	0.000	0.000
2 (1.55)	0.926	0.957	0.953	0.987	0.980	0.987	0.977	0.922	0.963	0.958	0.960	0.985	0.969	0.959	0.967	1.000
3 (1.10)	0.051	0.028	0.044	0.007	0.013	0.010	0.023	0.041	0.025	0.030	0.022	0.005	0.024	0.014	0.033	0.000
4 (0.72)	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000
N	235	199	148	76	224	192	86	148	163	132	112	97	127	243	60	33
χ^2	4.1	0.4	0.4	0.0	0.1	0.0	0.0	4.5	0.2	9.6*	42.6**	0.0	12.8*	20.4**	0.6	---
H_L	0.132	0.085	0.095	0.026	0.040	0.026	0.047	0.136	0.074	0.076	0.063	0.031	0.047	0.066	0.067	0.000
ME																
1 (1.31)	0.060	0.028	0.098	0.026	0.016	0.018	0.024	0.020	0.058	0.095	0.013	0.000	0.031	0.019	0.008	0.000
2 (1.10)	0.940	0.972	0.902	0.974	0.984	0.982	0.976	0.980	0.942	0.905	0.987	1.000	0.969	0.981	0.992	1.000
N	235	199	148	76	223	192	85	148	163	132	119	97	162	235	60	33
χ^2	200.7**	56.4**	37.5**	76.0**	99.3**	71.2**	27.2**	148.0**	95.3**	47.9**	52.2**	---	55.9**	102.4**	1.00	---
H_L	0.009	0.025	0.088	0.000	0.004	0.016	0.024	0.000	0.006	0.068	0.008	0.000	0.025	0.013	0.017	0.000
EST1																
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
N	235	196	148	76	205	149	58	148	163	130	93	95	138	211	50	32
IDH, MDH1, MPI, MNR1 MNR2, AGP1, AGP2, TO*																
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
N	61	25	28	34	25	15	20	64	52	34	20	34	24	25	20	15

Table II-2 cont'd

Average[4] H_L	0.108	0.100	0.105	0.104	0.112	0.107	0.097	0.117	0.110	0.110	0.123	0.106	0.129	0.107	0.107	0.097
SE	0.057	0.055	0.054	0.052	0.064	0.060	0.053	0.061	0.059	0.055	0.063	0.054	0.066	0.058	0.056	0.063
Average[5] H_L	0.302	0.279	0.295	0.292	0.313	0.300	0.273	0.327	0.308	0.307	0.345	0.296	0.363	0.300	0.301	0.273
SE	0.126	0.123	0.114	0.141	0.145	0.137	0.116	0.125	0.126	0.113	0.130	0.130	0.138	0.128	0.118	0.157

[1]At each site adult beetles were collected from beneath bark of trees in July of the latter year unless otherwise noted.
[2]Beetles were reared from slabs cut from infested trees in late August and thus did not overwinter.
[3]Numbers in parentheses are Rf values calculated in reference to isoenzymes of a corn hybrid "Spancross".
[4]Data for each locus is identical.
[5]Averaged over all 14 loci.
[6]Averaged over all polymorphic loci.
Tests were significant at the 95% (*) or 99% (**) level.

Table II-3. Nei's (1972) genetic identity values for mountain pine beetle populations from eight sites in Alberta and British Columbia.

	WPC	JC	YC	SR	SNR	MP	PR
JC	0.997						
YC	0.982	0.995					
SR	0.990	0.999	0.993				
SNR	0.995	0.988	0.979	0.989			
MP	0.998	0.982	0.998	0.994	0.993		
PR	0.984	0.995	0.985	0.979	0.995	0.994	
SM	0.980	0.993	0.995	0.997	0.987	0.993	0.983

Table II-4. Tests of homogeneity of allele frequencies and F-tests of individual heterozygosity (H_I) of mountain pine beetles among sites.

		EST2		AAT1		PGM		PGI		ME		
Site	Groups	N	χ^2	N	χ^2	N	χ^2	N	χ^2	N	χ^2	F
WPC	1,2,8	579		578		482		582		582		
JC	9,11	256		301		216		275		282		
YC	4	76		66		66		76		76		
SR	12	94	55.2***	95	10.7	95	74.9***	97	314.0***	97	21.1**	1.12
SNR	13	138	df=21	158	df=7	39	df=7	127	df=7	162	df=7	df=1,1084
MP	14,15	261		318		133		303		295		
PR	5,7	263		305		148		310		308		
SM	16	32		33		29		33		33		

Tests were significant at the 95% (*), 99% (**), or 99.9% (***) level.

Table II-5. Tests of homogeneity of allele frequencies, Nei's (1972) genetic identity (I) values and F-tests of individual heterozygosity (H_I) of mountain pine beetles among years (=generations) at each of four sites.

			EST2		AAT1		PGM		PGI		ME			
Site	Year	Group	N	χ^2	N	χ^2	N	χ^2	N	χ^2	N	χ^2	I	F
WPC	84/85	1	235	2.1	235	4.6*	199	1.0	235	3.1	235	5.1	0.997	0.5
	85/86	2	196	df=3	195	df=1	145	df=1	199	df=1	199	df=1		df=1,345
PR	85/86	5	205	3.0	220	0.1	99	0.1	224	0.4	223	0.4	0.994	0.3
	86/87	7	58	df=3	85	df=1	49	df=1	86	df=1	85	df=1		df=1,127
JC	84/85	9	163	21.2***	163	0.1	153	1.0	163	0.0	163	7.7**	0.996	0.5
	85/86	11	93	df=3	138	df=1	63	df=1	112	df=1	119	df=1		df=1,175
MP	85/86	14	211	2.3	259	0.1	74	7.7**	243	1.9	235	0.7	0.996	0.4
	86/87	15	50	df=3	59	df=1	59	df=1	60	df=1	60	df=1		df=1,88

Tests were significant at the 95% (*), 99% (**), or 99.9% (***) level.

Table II-6. Tests of homogeneity of allele frequencies, Nei's (1972) genetic identity (I) and F-tests of individual heterozygosity (H_I) among sexes for seven groups of mountain pine beetles.

		EST2		AAT1		PGM		PGI		ME			
Group	Sex	N	χ^2	N	χ^2	N	χ^2	N	χ^2	N	χ^2	I	F
1	M	85	2.6	85	0.9	80	0.9	85	0.3	85	6.2*	0.998	0.0
	F	150	df=3	150	df=1	119	df=1	150	df=1	150	df=1		df=1,199
3	M	56	2.1	57	0.0	54	1.1	57	0.3	57	2.4	0.998	0.4
	F	91	df=3	91	df=1	88	df=1	91	df=1	91	df=1		df=1,137
4	M	31	5.4	31	0.2	26	0.2	31	1.5	31	0.1	0.996	5.4*
	F	45	df=3	45	df=1	40	df=1	45	df=1	45	df=1		df=1,66
8	M	58	6.9	58	0.1	53	0.4	58	0.6	58	0.1	0.999	0.1
	F	90	df=3	90	df=1	85	df=1	90	df=1	90	df=1		df=1,138
9	M	60	0.7	60	1.8	55	1.0	60	2.1	60	2.2	0.996	1.6
	F	103	df=3	103	df=1	98	df=1	103	df=1	103	df=1		df=1,153
10	M	46	10.4*	46	0.0	46	0.7	47	0.0	47	7.2**	0.997	2.9
	F	84	df=3	85	df=1	82	df=1	85	df=1	85	df=1		df=1,125
12	M	34	7.8*	34	0.2	34	0.6	36	1.7	36	---	0.996	1.8
	F	60	df=3	61	df=1	61	df=1	61	df=1	61			df=1,93

Tests were significant at the 95% (*) or 99% (**) level.

Table II-7. Tests of homogeneity of allele frequencies, Nei's (1972) genetic identity (I) and F-tests of individual heterozygosity (H_I) among mountain pine beetles collected before and after winter at each of two sites.

Site	Host	Time of collection	Group	EST2 N	EST2 χ^2	AAT1 N	AAT1 χ^2	PGM N	PGM χ^2	PGI N	PGI χ^2	ME N	ME χ^2	I	F
JC	LMP	Before	10	130	4.5	131	2.2	128	4.7*	132	1.4	132	0.2	0.995	0.0
		After	11	93	df=3	138	df=1	63	df=1	112	df=1	119	df=1		df=1,267
PR	LPP	Before	6	149	11.3**	190	14.7***	84	4.5*	192	0.3	192	16.0***	0.982	0.9
		After	7	58	df=3	85	df=1	49	df=1	86	df=1	85	df=1		df=1,118

Tests were significant at the 95% (*), 99% (**), or 99.9% (***) level.

Table II-8. Tests of homogeneity of allele frequencies, Nei's (1972) genetic identity (I) values and F-tests of individual heterozygosity (H_I) of mountain pine beetles among individual trees of the same species within a site.

Group	Host	No. of trees	EST2 N	EST2 χ^2	AAT1 N	AAT1 χ^2	PGM N	PGM χ^2	PGI N	PGI χ^2	ME N	ME χ^2	I	F
1	LPP	4	235	13.6 df=9	235	2.7 df=3	199	1.5 df=3	235	9.0* df=3	235	2.3 df=3	0.999	2.1 df=1,197
8	LMP	5	148	23.8* df=12	148	6.1 df=4	138	7.5 df=4	148	4.1 df=4	148	9.8* df=4	0.999	1.6 df=1,138
9	LMP	5	163	25.8* df=12	163	13.6* df=4	153	13.5* df=4	163	7.4 df=4	163	6.4 df=4	0.999	0.7 df=1,153

Tests were significant at the 95% (*) level.

Table II-9. Tests of homogeneity of allele frequencies, Nei's (1972) genetic identity (I) values and F-tests of individual heterozygosity (H_I) of mountain pine beetles among hosts within a site.

			EST2		AAT1		PGM		PGI		ME			
Site	Host	Group	N	χ^2	N	χ^2	N	χ^2	N	χ^2	N	χ^2	I	F
WPC	LPP	1	235	9.6*	235	0.2	199	21.8***	235	0.5	235	6.6*	0.999	4.0*
	LMP	8	148	df=3	148	df=1	138	df=1	148	df=1	148	df=1		df=1,335
JC	LPP	3	147	6.9	148	2.9	142	0.7	148	0.7	148	0.0	0.999	0.2
	LMP	10	130	df=3	131	df=1	128	df=1	132	df=1	132	df=1		df=1,264

Tests were significant at the 95% (*), 99% (**), or 99.9% (***) level

Table II-10. Discriminant function coefficients for seven morphological characters measured on 70 male and 70 female *D. ponderosae* from Alberta. The characters are listed in the order of their importance to discrimination among groups.

Character	Discriminant function coefficient
pronotum length	0.571
head width	0.521
distance between antennae	-0.722
eye length	-0.336
eye width	-0.267
pro-tibia length	-0.156
pro-femur length	-0.328
constant	-3.855

cannonical correlation: 0.86

percent of grouped cases correctly classified: 96.4

Table II-11. Analyses of variance comparing *D. ponderosae* among sexes, sites and hosts for 12 morphological characters.

Character	Sexes	Sites	Hosts
pronotum length	116.7***	0.4	1.3
pronotum width	77.2***	1.0	0.5
head width	82.6***	0.3	2.0
distance between antennae	37.1***	0.6	1.7
distance between eyes	59.0***	0.8	0.9
eye length	17.9***	3.1*	0.2
eye width	3.5	0.3	2.8
elytra length	55.9***	2.4	0.1
metepisternum length	61.5***	1.8	0.2
distance between meso-coxae	44.1***	3.2*	2.0
pro-tibia length	16.5***	0.6	2.2
pro-femur length	17.3***	1.4	2.5
degrees of freedom	1, 138	3, 136	1, 78

tests were significant at the 95% (*), 99% (**), or 99.9% (***) levels; only beetles from the White Pine Coulee site were used to make comparisons among hosts.

Table II-12. Discriminant function coefficients for nine morphological characters measured on *D. ponderosae* collected from four sites: White Pine Coulee (80), Jim Creek (20), Skyline Road (20) and Yarrow Creek (20). The characters are listed in the order of their importance to discrimination among groups.

Characters	Discriminant function coefficients		
	1	2	3
pronotum length	-0.188	-0.054	0.403
head width	-0.584	0.022	-0.343
eye length	0.519	0.222	0.430
eye width	-0.360	0.433	-0.946
elytra length	0.191	0.047	-0.001
metepisternum length	0.427	-0.161	-0.689
distance between meso-coxae	0.582	0.521	0.326
pro-tibia length	-0.272	0.498	0.308
pro-femur length	0.024	-0.752	0.470
constant	-7.149	-2.147	-0.833

cannonical correlation: function 1- 0.60; 2- 0.37; 3- 0.25

percent of grouped cases correctly classified: 54.3

Table II-13. Discriminant function coefficients for ten morphological characters measured on 40 *D. ponderosae* collected from LPP and 40 from LMP at the White Pine Coulee site in Alberta. Characters are listed in the order of their importance to discrimination among groups.

Character	Discriminant function coefficient
pronotum length	0.250
pronotum width	-0.250
head width	0.469
distance between antennae	0.559
distance between eyes	-0.385
eye width	0.739
elytra length	-0.186
metepisternum length	-0.500
distance between meso-coxae	0.606
pro-tibia length	0.188
constant	-1.076

cannonical correlation: 0.54

percent of grouped cases correctly classified: 70.0

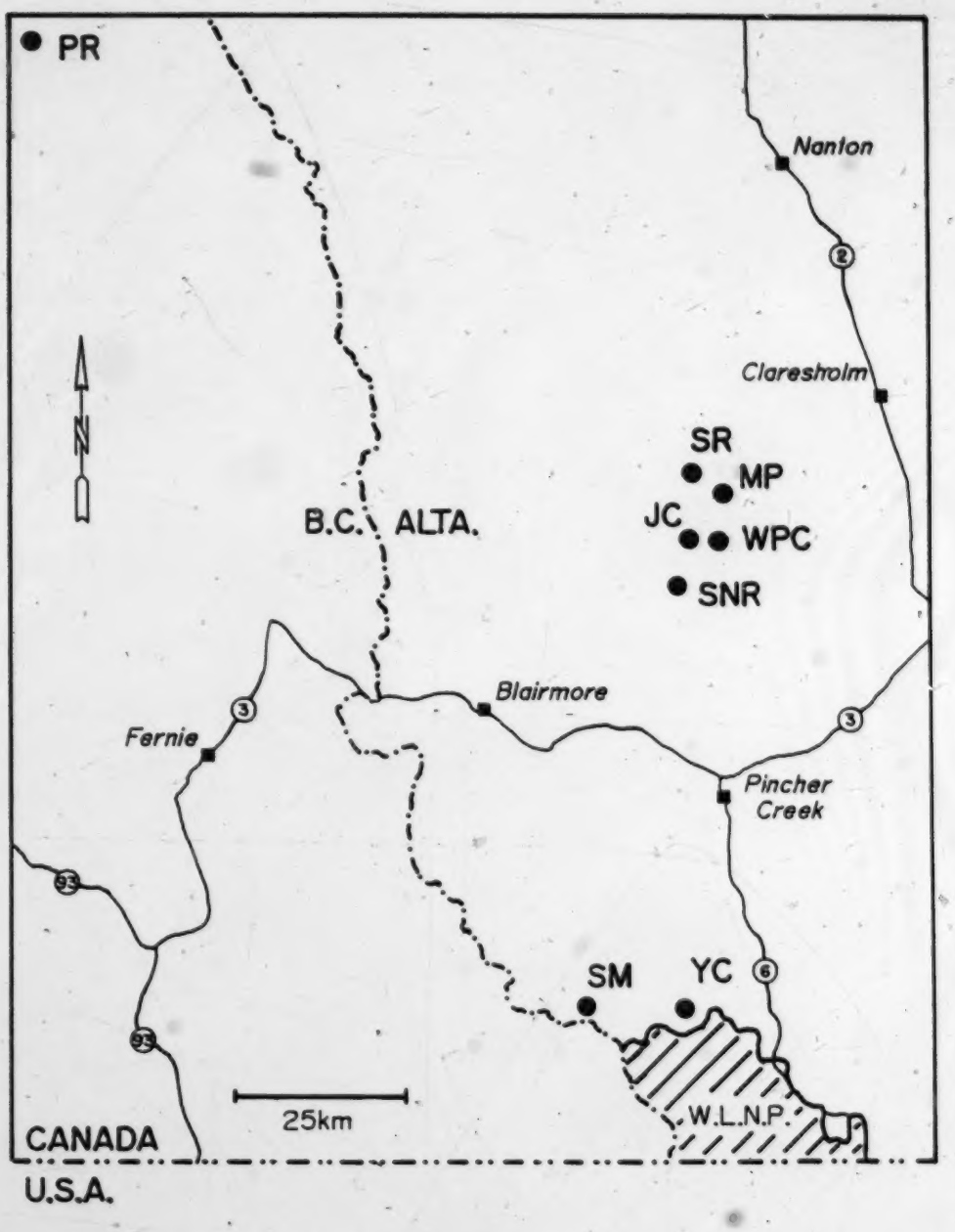

Fig. II-1. Sites at which D. ponderosae allozyme variation was sampled in Alberta and eastern British Columbia from 1985 to 1987. SR- Skyline Road; MP- Muddypound Creek; JC- Jim Creek; WPC- White Pine Coulee; SNR- Snake Road; YC- Yarrow Creek; SM- Sage Mountain; PR- Palliser River; W.L.N.P.- Waterton Lakes National Park.

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III. CONTROLLED BREEDING STUDIES

A. Introduction

The MPB infests 13 native and several exotic pine species, as well as other conifers, in western North America (Furniss and Schenk 1969; McCambridge 1975; Smith *et al.* 1981; Wood 1982). Under epidemic conditions, any or all acceptable host species may be attacked in a given geographical region (Wood 1982) and host switching commonly occurs (Richmond 1933). However, during endemic conditions mountain pine beetle populations may exhibit preference for one host species even when other acceptable species are available (Baker *et al.* 1971; Wood 1982). Similar observations about host preference by *D. ponderosae* caused A.D. Hopkins to propose the 'Host Selection Principle' (Hopkins 1916, 1917): "....a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted". However, most evidence suggests that this principle does not hold true for scolytids (Wood 1963).

Epidemic bark beetle populations are of obvious interest to entomologists and forest managers. However, from an evolutionary perspective, endemic populations are also of great interest with regard to adaptive radiation and speciation among scolytids. The possible restriction of gene flow between host-adapted endemic populations of

beetles, coupled with differential selection pressures mediated by chemical and physical differences between host species, provide essential ingredients for accumulation of host-adapted genes (Sturgeon and Mitton 1982). As to whether accumulation of host-adapted genes will, by itself, ultimately lead to speciation is a matter of contention among evolutionary biologists (Stebbins and Ayala 1981). However, the consolidation of gene complexes adapted to different host plants in combination with genetic transilience (Templeton 1980) may increase the probability of host race formation and speciation (Sturgeon and Mitton 1982).

Because reproductive isolation is a necessary prerequisite for speciation, one would expect to see evidence of pre- and/or post-mating reproductive isolation mechanisms preceeding the formation of host races or sibling species (Wood 1980). These studies were initiated to examine the possibility of reproductive isolation among MPB populations from LPP and LMP. Here I report information about relative compatibilty and fecundity of beetles cross-bred with respect to juvenile host and about the development, mortality and fertility of their progeny.

B. Materials and Methods

The most recent outbreak of *D. ponderosae* in Alberta was first detected in LPP in 1977 (Cerezke and Gates 1983) and in LMP and whitebark pine in 1980 (Hiratsuka *et al.* 1981). Beetle populations started to decline around 1983 (Moody and Cerezke 1984) and were at endemic levels in 1987 (personal observation).

Beetle collection and bolt preparation. In late June and early July 1986, adult *D. ponderosae* were collected by hand and with emergence traps from LMP at three localities in the Porcupine Hills of southwestern Alberta. Beetles were similarly collected from LPP at one locality in the Porcupine Hills as well as 70 to 80 km northwest, in the Palliser River basin of eastern British Columbia. Beetle populations in LPP and LMP in Alberta were declining or endemic, whereas the Palliser River population was epidemic. Upon collection beetles were sexed using the method of Lyon (1958), and stored at 4°C for three to seven days in petri dishes lined with moistened filter paper. Before mating beetles were removed from cold storage and kept at room temperature for about 12 hours.

Thirty LPP and 30 LMP bolts (75 cm long, 30-55 cm diameter, 2.5-3.5 mm phloem thickness) were cut from several localities and numerous trees in the Porcupine

Hills two days before use. Bolts were chosen to standardize phloem thickness using measurements averaged from both ends of each bolt. The bark surface of 15 bolts of each species was divided into four equal sections with a chainsaw by cutting four longitudinal slashes, which penetrated the wood about 5 mm. The total area of each section was similar within bolts but ranged from 2000 to 2400 cm^2 between bolts. Progeny were allowed to mature and emerge. Slashing the bolts prevented mixing of larvae from adjacent galleries, thus enabling more accurate measures of F_1 development and mortality. The other 15 bolts of each species were not slashed since they were to be debarked after completion of gallery construction (six weeks) for measurement of egg gallery length and fecundity. Thus, intermixing of larvae was of no consequence. Hot paraffin was used to coat the ends and slashes of the bolts which were then stored indoors at 22-24 °C.

P_1 crosses. Equal numbers of LMP beetles from each of the three collection localities were pooled and used randomly for the crosses. LPP beetles collected from the Porcupine Hills were few in number and were used for only 12 replications of the LPP (female) X LPP (male) crosses in each host species. Beetles from the Palliser River basin were used for the rest of the LPP X LPP crosses as well as for all of the LPP X LMP and LMP X LPP crosses in

each host. One pair of beetles from each of the four mating combinations was introduced to each of the 60 bolts. To facilitate introduction, four holes, spaced equidistantly around the circumferance of the bolt, were punched into the bark and phloem of each bolt about 2 cm from its base. A female was inserted into each hole which was then covered by a gelatin capsule. A male was introduced into each hole one day later. Bolts were stored at room temperature.

The 15 'unslashed' bolts of each species were debarked after six weeks when egg gallery construction was completed. Egg gallery length and the number of egg niches (index of fecundity) was measured for each gallery. The number of egg niches was regressed on gallery length for each of the four crosses in each host and the resulting equations were used to estimate egg niches from gallery length measured in the slashed bolts. Egg niches could not be counted directly in the slashed bolts because feeding of the larvae and brood adults destroyed many of them.

Each gallery in the other 15 'slashed' bolts of each species was individually caged and emerging F_1's were collected every two to three days. Once emergence was completed those bolts were also debarked. Gallery length and the number of pupal chambers from which beetles emerged was tallied for each gallery. Expected fecundity

for each beetle pair was estimated as explained above. Brood (F_1) mortality was calculated for each gallery as the difference between the number of emerged beetles and expected fecundity. For each gallery, the number of days from the time that the male parent was introduced until 50% of progeny had emerged (E50) was calculated and used as an index of F_1 development rate.

F_1 crosses. The F_1's produced by the crosses set-up in 1986 were not inter-bred because of difficulties in obtaining fresh bolts. However, cross-breeding experiments similar to those of 1986 were done in 1985 using beetles collected from four localities in the Porcupine Hills. Because of the poor experimental design of the 1985 studies, most of the data collected were not reliable and were not subjected to statistical analysis. However, enough F_1's were produced to allow us to set up 14 crosses (Table III-6), 10 replicates per cross. Five pairs, of different parental combinations, were placed in each of 28 'unslashed' LPP bolts (60 cm long, 35-45 cm diameter, 2.5-3.5 mm phloem thickness). LMP bolts were not available. Bolts were debarked after two months at room temperature. Egg gallery length and the number of larval galleries (index of fecundity) were measured for each egg gallery. Egg niches could not be counted because large portions of the sides of egg galleries were often destroyed by feeding larvae.

Dry weight and fat content studies. In 1986, dry weight and percent fat content was determined for 27 to 60 F_1's from each cross. Upon emergence F_1 beetles were immediately stored at -20°C until processed. Beetles were dried in an incubator at 47°C for 24 hours and then in a sealed dessicator over phosphorus pentoxide for 72 hours. Dry weight was determined using a Cahn 26 automatic electrobalance (precision = ± 0.005 mg). To extract fat, beetles were individually placed in 5 ml glass vials filled with petroleum ether. Vials were placed at 47°C for 72 hours. The old petroleum ether was removed and replaced with fresh solvent every 24 hours. Beetles were then dried and weighed as before, sexed, and pronotal width was measured with an ocular micrometer. Fat content was calculated as percent decrease in dry weight.

Statistical analysis. The MINITAB statistical package (Ryan *et al.* 1985) was used for analyses of variance, χ^2 tests and regressions. Because of the extremely low fat content of some beetles, outliers in the data set were removed. Suspected outliers were tested using the statistic $T = x - u/\sigma$, where x is the suspected outlier and u and σ are, respectively, the mean and standard deviation of the data set excluding the suspected outlier. T was then compared to the upper significance bounds of the standardized extreme deviation (Sachs 1984 - Table 56).

C. Results

P_1 crosses

Effect of LPP beetle source on measured parameters. The use of LPP beetles from two relatively widely separated sources that differed markedly in population level and genetics (Chapter II) necessitated an analysis of the effect of LPP beetle source on each of the parameters measured in this study. The 24 pairings (12 in each host species) of LPP X LPP which utilized LPP beetles from the Porcupine Hills (endemic population) were thus compared to the other 36 pairings of the same cross which utilized LPP beetles collected from the Palliser River basin (epidemic) population. There was no effect of LPP beetle source on any of the parameters (Table III-1) and so data for LPP beetles were pooled in subsequent analyses.

Reproductive success of P_1's. The reproductive success (% of pairs of each P_1 cross that produced fertile eggs) data were pooled for the 1985 and 1986 experiments (Table III-2). Reproductive success varied between 78 and 92% among crosses. There was no significant difference in reproductive success among the crosses within each host (Table III-2) or between hosts ($\chi^2 = 0.15$, df = 1, P = 0.99). The two crosses involving parents that both originated from the same host species

had the highest percent reproductive success of all crosses in both LMP (not significant) and LPP (marginally significant $\chi^2 = 4.05$, df = 1, $p < 0.05$).

Gallery length and egg niches. There was no difference in egg gallery length among the crosses in LMP ($F = 0.79$, df = 3, 88, $P = 0.50$) or among those in LPP ($F = 0.84$, df = 3, 103, $P = 0.48$). The average gallery length for each cross (except the LPP X LMP cross) in LPP was longer than for the corresponding cross in LMP, but the difference was significant for only the LPP X LPP cross (Table III-3a). Overall, gallery length for pooled data from LPP was significantly greater than for LMP (Table III-3a).

For each cross there was no significant difference in estimated beetle fecundity (number of egg niches) between hosts (Table III-3b). However, overall the number of egg niches (reproductive output) per cm of gallery length was significantly higher for crosses in LMP than for those in LPP (Table III-3c).

Generally, crosses involving LMP females showed the highest fecundity in both hosts, the only exception being the LMP X LMP cross in LPP. In LMP bolts, LMP females were more fecund than LPP females ($F = 10.06$, df = 1, 43, $P < 0.01$) but there was no difference in LPP bolts ($F = 2.63$, df = 1, 49, $P = 0.12$). However, LMP females

produced a higher number of egg niches per cm of gallery length than LPR females in both LPP ($F = 6.69$, $df = 1, 49$, $P < 0.05$) and LMP ($F = 6.33$, $df = 1, 43$, $P < 0.05$) bolts.

Development and mortality of F_1's. The development index (E50) averaged about 83 days for all crosses combined in both LMP and LPP, and F_1 mortality in the two hosts averaged 67 and 65%, respectively (Table III-4). In LMP bolts, brood of LMP females developed faster ($F = 7.12$, $df = 1, 45$, $P < 0.05$) and with less mortality ($F = 16.87$, $df = 1, 45$, $p < 0.001$) than brood of LPP females. However, in LPP bolts the source of the P_1 female had no effect on development ($F = 0.03$, $df = 1, 54$, $P = 0.99$) or mortality ($F = 0.35$, $df = 1, 54$, $P = 0.92$) of F_1's. The source of the P_1 male had no apparent effect in either host.

The principal causes of mortality among F_1's seemed to be fungal pathogens, although dehydration may have had an important effect toward the end of development in LPP. Also, perhaps a portion of larval mortality resulted from inability to detoxify compounds present in the phloem of the two host species (Sturgeon and Mitton 1982).

Dry weight and fat content of F_1's. For all crosses combined, the dry weight of females ($\bar{X} \pm SD$, 4.08 mg ± 1.142) was higher ($F = 94.80$, $df = 1, 361$, $p < 0.001$)

than that of males (3.08 mg ± 0.737). Similarly, the percent fat content of females (23.3 mg ± 7.28 %) was higher ($F = 75.53$, $df = 1, 361$, $p < 0.001$) than that of males (17.0 mg ± 6.41). The progeny of all four crosses in LMP had higher average dry weights (and three of the four were significantly higher) than the corresponding crosses in LPP (Table III-5). However, this pattern was not evident for percent fat content of F_1's (Table III-5). Additionally, the source of the maternal parent had no significant effect on dry weight or fat content of the F_1's. However, progeny from the two crosses involving parents that originated from the same host species had a higher fat content than the two crosses involving parents from different host species, in both LPP ($F = 4.68$, $df = 1, 188$, $P < 0.05$) and LMP ($F = 11.47$, $df = 1, 171$, $P < 0.01$). The same pattern was evident with respect to dry weight for the crosses in LMP ($F = 7.90$, $df = 1, 171$, $P < 0.01$) but not in LPP ($F = 0.43$, $df = 1, 188$). Thus, host species appeared to have a direct effect on dry weight and an indirect effect on fat content mediated by parental compatibility.

F_1 crosses.

All 14 F_1 crosses were fertile (Table III-6). Crosses A-G involved F_1's that were reared in LMP and crosses H-N involved F_1's that were reared in LPP. There was no significant variation in reproductive success, egg

gallery length, number of larval galleries per egg gallery or number of larval galleries per cm of egg gallery length either within or among the two groups of F_1 crosses.

Experimental designs for the 1985 F_1 crosses and the 1986 P_1 crosses were quite different. Thus the two sets of crosses cannot be compared. However, the four 1985 P_1 crosses that were set up in LPP can be used as a reference for comparing the relative performance of the F_1 crosses (all set up in LPP) in 1985. The two generations did not differ in reproductive success (χ^2 = 0.23, df = 1, P = 0.66) or egg gallery length (F = 0.14, df = 1, 207, P = 0.95). However, the number of larval galleries per egg gallery (66.2 ± 17.13) and the number of larval galleries per cm of egg gallery (1.4 ± 0.60) for the P_1 crosses was at least twice as high as for the F_1 crosses (Table III-6). Since the number of egg niches could not be counted I cannot be sure that this represents a real difference in fecundity between the t[illegible] generations or differential egg mortality.

D. Discussion

Reproductive output was measured in terms of parental reproductive success and fecundity as well as development, survival and fertility of their progeny. Three factors, all directly or indirectly related to the

host, appeared to influence reproductive output of the various crosses in this study: (1) the host species in which the progeny were reared (pure host effect), (2) the host species in which the parental female was reared before mated (maternally-mediated host effect), and (3) whether both parents originated from the same or different host species (compatibility-mediated host effect).

(1) Pure host effects. These were evident for egg gallery length, number of egg niches per cm of egg gallery and F_1 dry weight (Tables III-3, III-5). Since phloem thickness was controlled in these studies, the significantly higher number of egg niches per cm of gallery length (which reflects the egg output per unit of phloem ingested by females) for the crosses in LMP, as compared to the same crosses in LPP, suggests that LMP phloem is more nutritious than LPP phloem. Given such nutritional differences between LPP and LMP phloem one might also expect F_1's to have faster development, better survival, greater dry weight and higher percent fat content in the species with the more nutritious phloem. However, only F_1 dry weight was strongly affected in the expected direction by host species (Table III-5).

Based on the relative reproductive output of *D. ponderosae* that were collected from LPP and transferred to three other pine species, Amman (1982) suggested a

difference in the nutritional quality of the phloem among the four species. Overall, the two soft pine species, whitebark pine and western white pine (*Pinus monticola* Douglas), seemed to be better for *D. ponderosae* reproduction than the two hard pine species, LPP and ponderosa pine (*Pinus ponderosa* Laws.). Similarly, my results indicate that LMP, another soft pine, is more suitable for *D. ponderosae* reproduction and development than LPP.

The basis of nutritional differences between phloem of different tree species is not clear. Difference in phloem quality between LPP and LMP may be either quantitative (eg. difference in phloem density) or qualitative. Differences in phloem density are best measured directly. However, phloem density may also be reflected by the rate of egg gallery elongation in the two hosts, with galleries being elongated faster in less dense phloem. Although rates of egg gallery elongation were not measured, the fact that average egg gallery length in LPP was significantly greater than in LMP (Table III-3) may indicate that LPP has less dense phloem. However, there were no significant differences in the length of *D. ponderosae* egg galleries produced in LPP and LMP in the field (Chapter IV). Therefore, an hypothesis which includes qualitative nutritional differences in phloem is favoured.

(2) Maternally-mediated host effects. Generally, parental females were more fecund and their progeny developed faster and survived better in the host species where the P_1 female underwent larval development (Tables III-3, III-4). Since in most cases differences were not statistically significant it appears that maternally-mediated host influences were not strong.

In theory it seems reasonable that insects practicing host fidelity would have higher fecundity since they have already adjusted to the chemical/physical environment of their host and thus can put more energy into the production of more and/or better quality eggs than insects subjected to the higher levels of physiological stress that likely accompanies a switch in host species. Thus, maternally-mediated host effects may simply be explained as a consequence of superior quality eggs that hatch sooner and/or produce larger first instar larvae. However, increased reproductive output associated with host fidelity is not always evident for *D. ponderosae*. Amman (1982) showed that, of four pine species used to rear *D. ponderosae*, LPP was the least suitable even though the beetles used in the study originated from LPP. However, phloem thickness was not controlled in that study.

It is interesting that P_1 females collected from LMP not only did better than females collected from LPP, in

terms of fecundity as well as development and survival of their progeny, in LMP, but also did just as well or better in these characteristics in LPP bolts. There was no significant difference in size (pronotum width) between LPP and LMP parental females ($F = 2.24$, $df = 1, 68$) or males ($F = 0.00$, $df = 1,60$), so a size effect on reproductive output can be discounted. We suggest that LMP is a more restrictive host environment, selecting larvae with genes for superior detoxification systems (Sturgeon and Mitton 1982) or better nutritional capabilities (e.g. assimilation). It is also possible that progeny from LMP females are more plastic with respect to development owing to maternally inherited cytoplasmic factors.

(3) Compatibility-mediated host effects. Source of parental beetles appeared to influence reproductive success. The two P_1 crosses involving males and females that were reared in the same host species (pure crosses) had better success than the two crosses involving males and females from different host species (mixed crosses) (Table III-2). Although this trend was evident among crosses in both LPP and LMP, it was only significant in LPP. Behavioural incompatability (acoustic, chemical or otherwise) between males and females and/or morphological, physiological or genetic incompatibility of eggs and sperm may have reduced reproductive success

among mixed crosses.

A compatibility-mediated influence on F_1 dryweight and percent fat content was also evident. Progeny of P_1 crosses involving parents from the same host species were heavier (only among crosses in LMP) and had a significantly higher percent fat content (among crosses in both LMP and LPP) than progeny of P_1 crosses involving parents from different host species. There was no such influence on F_1 development and mortality (Table III-5) but it is not necessary that an effect be manifested among all measures of reproductive performance since they are under control of different genes.

The degree of genetic divergence between populations of an insect species on different host species is a balance between the differential selective effects provided by the different hosts (and their environment) and the homogenizing effects of gene flow between the insect populations. This study and additional fieldwork (Chapter IV) show direct and indirect influences of host species on *D. ponderosae* that could select for reproductive isolation. However, there was no evidence of any pre- or post-mating reproductive barriers to gene flow between populations in LMP and LPP. There are three reasons why such reproductive barriers between the two populations may not be reinforced: lack of sufficient host fidelity in host recognition and selection systems,

no effective differences in mate recognition systems (i.e., no assortive mating) and no phenological differences between insects in different hosts.

A necessary prerequisite for formation of barriers to gene flow between insect populations utilizing different host species is host fidelity. Population genetic models indicate that an exchange of only one beetle per generation between two populations may be enough to keep two populations from diverging (Slatkin 1987). Population genetic studies indicate significant genetic divergence at three of five polymorphic loci among co-occurring populations of *D. ponderosae* in LMP and LPP at one site in Alberta (Chapter II), at two of five polymorphic loci among co-occurring populations in LMP, LPP and ponderosa pine in Colorado (Sturgeon and Mitton 1986), and at two of six loci among co-occurring populations in LPP and ponderosa pine in Idaho (Stock and Amman 1983). In all of these studies beetles that were sampled were collected from the host where the juveniles developed before emergence. Therefore, the possibility that the observed significant genetic divergence between beetles in different host species represents differential host selection, and thus subdivision of *D. ponderosae* populations along host lines, is confounded with the possibility that it may simply reflect the different selection pressures in each tree species. Although there

was likely some host fidelity among the declining beetle populations in LPP and LMP examined in the Alberta study, there was undoubtedly enough interbreeding to prevent genetic divergence of beetles along host lines (Chapter II).

For insects utilizing several host species, assortive mating contributes to the formation of reproductive barriers (Paterson 1985). In *D. ponderosae* mating occurs on the host after host selection by the female (Amman and Cole 1983). Mate recognition and selection involves initial response of males to female-produced pheromones followed by some interplay of physical, acoustic and likely chemical signals on the host (Amman and Cole 1983). Although host species has no effect on acoustic signals of *D. ponderosae* (Yandell 1984), one might expect significant host effects on *D. ponderosae* pheromones because they are synthesized from and synergized by host compounds. In fact, there are differences in pheromones among *D. ponderosae* from different hosts (McKnight 1979). As a prerequisite for assortive mating significant effective differences in the pheromones produced by beetles in different host species are required. Thus the pheromone system of *D. ponderosae* in LMP and LPP is worthy of investigation.

There are many examples of host effects on insect phenology which have led to reduced gene flow between

host-adapted populations (Bush 1969; Phillips and Barnes 1975; Mitter *et al.* 1979; Wood 1980). This study and fieldwork (Chapter IV) shows that *D. ponderosae* develops faster in LMP than LPP. One would then expect beetles in LMP to emerge and attack other hosts earlier than beetles in LPP. Although this was not the case at two sites in Alberta in 1985 (Chapter IV), it was in 1984 (Smith 1984) and 1986 (Chapter IV). It could then be argued that the emergence/ attack periods of beetles reared in LMP and LPP might gradually diverge with each successive generation, if there was strong host fidelity, establishing a phenological barrier to gene flow. This has not occurred for *D. ponderosae* populations in Alberta because of a lack of strong host fidelity.

Thus any combination of the above factors may account for the apparent lack of reproductive barriers between *D. ponderosae* populations in LMP and LPP in Alberta. However, on the basis of controlled-breeding studies alone one cannot rule out the existence of such isolation among *D. ponderosae* populations in different host species in the field for several reasons.

Firstly, P_1 males were forced into galleries with females and prevented from leaving by blocking the entrance. This probably disrupted normal courtship behaviour. To adequately determine if there is some courtship-based pre-mating reproductive isolation,

courtship and mate selection must be allowed to proceed normally.

Secondly, this experiment used cut bolts from which much of the resin drained before beetles were introduced. For this reason differences in selection pressures between LPP and LMP may not be as great in cut bolts as in standing trees. Hence, the reproductive performance of crosses in cut bolts might be quite different from what would occur in standing trees where selective forces may be more discriminatory. Some bark beetle species can produce brood in certain species of trees when felled but not when standing (Furniss *et al*. 1981; Safranyik and Linton 1983). Ideally, cross-breeding experiments might be repeated in standing trees.

Thirdly, the *D. ponderosae* populations used as sources of beetles for these studies were epidemic or declining. Although there was some degree of host fidelity, significant genetic exchange between beetle populations in LPP and LMP likely occurred up until 1986 when *D. ponderosae* populations in LPP collapsed and virtually disappeared. Therefore, it is unlikely that *D. ponderosae* populations in LMP had the opportunity to accumulate host-adapted genes which might affect the reproductive performance of the beetles when transplanted to LPP. It is more likely that host-adapted genes will accumulate in beetles during the endemic phase because

host preference/fidelity is thought to be stronger then (Baker *et al.* 1971; Wood 1982) and, hence, genetic exchange between host-adapted beetle populations is at a minimum. Repeating these breeding experiments with endemic beetle populations from LPP and LMP in a few years would provide an interesting comparison to this study. We might expect to find much stronger and pervasive host effects on reproductive success, fecundity, development and mortality than were evident from this study.

Table III-1. Comparison of the effects of source of LPP (P_1) beetles on each of eight measured parameters. Only data for the LPP X LPP cross were used for comparisons.

a. Reproductive success'					
Beetle source	successful galleries	unsucc. galleries	χ^2	df	P
Alta.	75	10	2.39	1	n.s.
B.C.	27	8			
b.	Mean egg gallery length (mm)		F	df	P
Alta.	65 (18.2)[2]		1.30	1,47	n.s.
B.C.	59 (21.3)				
c.	Mean no. egg niches per gallery				
Alta.	152 (61.2)		0.08	1,22	n.s.
B.C.	144 (67.1)				
d.	Mean no. niches per cm egg gallery				
Alta.	2.3 (0.6)		0.53	1,22	n.s.
B.C.	2.5 (0.9)				
e.	Mean development index of F_1's (E50)[3] (days)				
Alta.	85 (10.6)		0.00	1,21	n.s.
B.C.	85 (8.4)				
f.	Mean % mortality of F_1's				
Alta.	64.3 (11.9)		3.17	1,23	n.s.
B.C.	75.0 (16.3)				
g.	Mean dryweight of F_1's (mg)				
Alta.	3.68 (0.97)		0.99	1,114	n.s.
B.C.	3.89 (1.29)				

Table III-1 cont'd

h.	Mean % fat content of F_1's			
Alta.	23.1 (5.6)	0.58	1,114	n.s
B.C.	22.2 (7.5			

[1] % of pairs that produced fertile eggs.

[2] numbers in parentheses represent standard deviation.

[3] no. of days from the time that P_1's were mated until 50% of F_1's emerged.

Table III-2. Reproductive success (% of pairs of each cross that produced fertile eggs) of P_1 crosses. Data from 1985 and 1986 breeding studies are combined. χ^2 tests compare all four crosses within each host species.

Cross	Tree	% successful galleries (N)	
LMP f LMP m	LMP	88 (59)	
LMP f LPP m	LMP	78 (59)	$\chi^2 = 2.21$ df = 3
LPP f LMP m	LMP	81 (59)	P = 0.53
LPP f LPP m	LMP	83 (59)	
TOTAL	**LMP**	**83 (236)**	
LMP f LMP m	LPP	92 (60)	
LMP f LPP m	LPP	80 (60)	$\chi^2 = 4.38$ df = 3
LPP f LMP m	LPP	82 (60)	P = 0.22
LPP f LPP m	LPP	88 (60)	
TOTAL	**LPP**	**85 (240)**	

Table III-3. Average egg gallery length and fecundity (egg niches) of 1986 P_1 crosses.

a. Cross	Avg. gallery length (cm) LMP	LPP	F	df	P
LMP f LMP m	61.6 (16.0)	71.8 (21.2)	3.85	1,52	ns
LMP f LPP m	62.7 (17.9)	68.3 (17.6)	1.34	1,45	ns
LPP f LMP m	63.8 (51.9)	63.7 (25.0)	0.00	1,47	ns
LPP f LPP m	51.6 (18.3)	71.0 (17.1)	14.72	1,47	< 0.001
AVERAGE	**59.9** **(30.4)**	**69.0** **(20.4)**	**6.22**	**1,197**	**< 0.05**
b.	Avg. no. egg niches/gallery LMP	LPP			
LMP f LMP m	209.4 (82.4)	156.3 (51.6)	4.19	1,25	ns
LMP f LPP m	187.4 (74.0)	197.8 (30.0)	0.19	1,18	ns
LPP f LMP m	138.4 (62.4)	135.5 (67.9)	0.01	1,23	ns
LPP f LPP m	135.5 (53.6)	162.6 (72.2)	1.12	1,22	ns
AVERAGE	**165.2** **(73.5)**	**162.1** **(59.9)**	**0.05**	**1,94**	**ns**
c.	Avg. no. niches/cm gallery LMP	LPP			
LMP f LMP m	3.3 (0.7)	2.4 (0.5)	12.90	1,25	< 0.01
LMP f LPP m	2.9 (0.4)	2.7 (0.4)	0.81	1,18	ns

Table III-3 cont'd

LPP f LMP m	2.7 (0.5)	2.1 (0.3)	13.28	1,23	< 0.01
LPP f LPP m	2.6 (0.7)	2.2 (0.8)	1.57	1,22	ns
AVERAGE	**2.9** **(0.6)**	**2.4** **(0.6)**	**16.35**	**1,94**	**< 0.01**

' numbers in parentheses represent standard deviation

Table III-4. Development index (E50) and mortality of the 1986 F_1 generation.

a. Cross	E50' (days) LMP	LPP	F	df	P
LMP f LMP m	81.3 (6.1)[2]	83.3 (9.4)	0.34	1,25	ns
LMP f LPP m	79.1 (5.0)	82.7 (10.0)	1.35	1,25	ns
LPP f LMP m	85.3 (9.4)	81.5 (7.8)	1.10	1,22	ns
LPP f LPP m	88.0 (11.0)	83.4 (7.8)	1.37	1,23	ns
AVERAGE	83.1 (8.5)	82.8 (8.6)	0.03	1,101	ns

b.	Average mortality (%) LMP	LPP			
LMP f LMP m	62.6 (16.6)	56.2 (17.5)	0.92	1,25	ns
LMP f LPP m	54.5 (18.8)	69.1 (18.0)	4.25	1,25	<0.05
LPP f LMP m	76.4 (7.7)	66.9 (19.6)	2.44	1,22	ns
LPP f LPP m	76.0 (13.4)	67.2 (16.1)	2.06	1,23	ns
AVERAGE LPP	66.7 (17.2)	64.7 (18.0)	0.35	1,101	ns

[1] no. of days from the time that P_1's were mated until 50% of F_1's emerged
[2] numbers in parentheses represent standard deviation

Table III-5. Dryweight and percent fat content of the 1986 F_1 generation.

a. Cross	Average dryweight (mg) LMP	LPP	F	df	P
LMP f LMP m	4.22 (1.20)[1]	3.19 (0.91)	13.95	1,58	<0.01
LMP f LPP m	3.81 (0.96)	3.23 (0.91)	8.60	1,88	<0.01
LPP f LMP m	3.71 (1.23)	3.34 (0.92	2.94	1,95	n.s.
LPP f LPP m	4.26 (1.19)	3.34 (0.88)	23.05	1,114	<0.001
AVERAGE	**4.00** **(1.17)**	**3.29** **(0.90)**	**43.22**	**1,361**	**<0.001**

b. Cross	Average fat content[2] LMP	LPP	F	df	P
LMP f LMP m	22.9 (6.7)	18.6 (7.2)	5.60	1,58	<0.05
LMP f LPP m	16.5 (6.7)	20.0 (8.3)	4.74	1,88	<0.05
LPP f LMP m	20.1 (8.9)	18.8 (7.2)	0.67	1,95	n.s.
LPP f LPP m	22.0 (6.7)	23.3 (6.5)	1.19	1,114	n.s.
AVERAGE	**20.3** **(7.7)**	**20.5** **(7.5)**	**0.04**	**1,361**	**n.s.**

[1] numbers in parentheses represent standard deviation

[2] % of dryweight

Table III-6. Reproductive success (number of pairs that produced fertile eggs), average gallery length (GL), number of larval galleries per egg gallery (LG) and number of larval galleries per cm of egg gallery (LG/cm) for 1985 F_1 crosses. Crosses A-G involved F_1's that were reared from LMP and crosses H-N involved F_1's that were reared in LPP.

	Cross'	No. of galleries succ.	unsucc.	GL (cm)	LG	LG/cm
A	1f X 1m	8	2	42.6 (12.7)[a]	25.5 (9.7)	0.6 (0.2)
B	1f X 2m	10	0	49.3 (13.8)	23.7 (20.6)	0.5 (0.4)
C	1f X 3m	7	3	44.9 (7.4)	24.7 (10.5)	0.5 (0.2)
D	1f X 4m	8	2	40.3 (5.0)	29.4 (24.8)	0.7 (0.6)
E	2f X 1m	8	2	47.6 (16.0)	32.8 (18.5)	0.7 (0.4)
F	3f X 1m	9	1	40.8 (15.4)	28.1 (22.2)	0.7 (0.5)
G	4f X 1m	10	0	39.1 (10.3)	24.0 (12.6)	0.6 (0.3)
H	5f X 5m	8	2	41.5 (12.9)	29.4 (16.5)	0.7 (0.3)
I	5f X 6m	8	2	46.5 (8.1)	26.5 (22.7)	0.6 (0.4)
J	5f X 7m	3	7	45.3 (2.1)	21.7 (12.7)	0.5 (0.3)
K	5f X 8m	7	3	38.7 (12.0)	32.3 (40.3)	0.7 (0.8)
L	6f X 5m	8	2	44.3 (12.4)	40.9 (34.5)	0.9 (0.6)

Table III-6 cont'd

M	7f X 5m	8	2	43.9 (9.8)	44.6 (22.6)	1.0 (0.5)
N	8f X 5m	9	1	39.6 (24.6)	35.6 (34.1)	0.9 (0.7)
TOTAL/AVG.		111	29	**43.1** (12.9)	**30.1** (23.0)	**0.7** (0.5)

[1] numbers refer to P_1 cross combinations: 1- LMPf X LMPm in LMP, 2- LMPf X LPPm in LMP, 3- LPPf X LMPm in LMP, 4- LPPf X LPPm in LMP, 5- LMPf X LMPm in LPP, 6- LMPf X LPPm in LPP, 7- LPPf X LMPm in LPP, 8- LPPf X LPPm in LPP.

[2] numbers in parentheses are standard deviations.

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IV. POPULATION DYNAMICS

A. Introduction

One of the most important factors influencing the life of an endo-parasitic phytophagous insect is its host. Because different plant species differ chemically and physically, they can present markedly different selective environments to insects feeding on them (Bush 1969; Wood 1980). Differential selection pressures provided by different host species may cause genetic differentiation of an insect species along host lines, especially if there were some barrier to gene flow between insect populations in different hosts (Lanier and Burkholder 1974; Sturgeon and Mitton 1982). This could ultimately lead to speciation.

The MPB infests and feeds on the phloem of 13 native and several exotic pine species in western North America, often on several species within a region (Furniss and Schenk 1969; McCambridge 1975; Smith *et al.* 1981; Wood 1982). Host species can affect emergence, egg gallery characteristics, fecundity, development and mortality of *D. ponderosae* (Knight 1959; Reid 1962a, b, 1963; Schmid 1972; Billings and Gara 1975; Amman 1982; Safranyik and Linton 1982, 1983; Amman and Cole 1983). However, these studies were either done in cut bolts, which may not reflect conditions in standing trees, or results were

confounded with geographic variation. To date there have been no studies of the effect of host use on *D. ponderosae* populations in standing trees of different species at the same locality.

In the foothills of Alberta, *D. ponderosae* infests LPP and LMP, which are often inter-mixed (Alberta Forestry, Lands and Wildlife 1986). Population genetics studies indicate significant genetic divergence at three loci in co-occurring populations of *D. ponderosae* in LPP and LMP at one site, suggesting that the two populations may not be randomly mating or that there is selection of different genotypes in different hosts (Chapter II). The objective of this investigation was to assess phenological differences among *D. ponderosae* field populations associated with LPP and LMP and determine if observed differences may provide a barrier to gene flow between beetle populations in the two hosts. Additionally, this study compares the relative suitability of LPP and LMP for *D. ponderosae* reproduction, development and survival in the field and, thus, provide an interesting and necessary comparison with laboratory studies (Chapter III).

B. Materials and Methods

Study sites. Study sites were selected where infested LMP and LPP were in close proximity so as to

minimize the confounding effects of geographic variation. Two sites were studied in the Porcupine Hills of southwestern Alberta in 1985 and 1986: White Pine Coulee (49° 49' N, 113° 55' W) and Jim Creek (49° 48' N, 113° 59'W). Forest composition at both sites was mature and over-mature LPP, Engelmann spruce (*Picea engelmannii* Parry) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with LMP intermixed but occurring in more open stands predominantly near or on adjacent ridge tops. Epidemic mountain pine beetle populations had been active in the area since about 1982 (G. Smith- personnal communication) and were declining by 1985 (unpublished data). Beetle-infested LPP and LMP were separated by approximately 400 m at both localities. In general, infested LMP stands were about 50-150 m higher in altitude than infested LPP stands.

Emergence and host attack. In 1985, MPB emergence from three infested trees of each species at White Pine Coulee was monitored using 100 cm^2 circular emergence traps (McClelland *et al.* 1978). Four traps were placed at each of two heights, 0.5 m above ground level and half-way up the infested bole (2-3 m above ground level for LMP and 3-4 m for LPP), on each tree and emptied every 3-4 days. Beetles were sexed using the method of Lyon (1958). The mean diameter at breast height of the sampled LMP was 32.7 cm and LPP was 36.2 cm.

Host colonization was monitored on three trees of each species at Jim Creek and three LPP and two LMP at White Pine Coulee. Every 3-4 days the number of new attacks was counted within fixed 100 cm^2 sampling areas. Sampling areas were located in each cardinal direction at 0.5 m from the ground and at 1 m intervals along the bole thereafter. After cessation of host attack, emergence traps were placed on each tree to monitor re-emergence.

Fecundity, development and mortality. Two trees of each species at each site were used to study fecundity, development and mortality. Following start of host colonization, samples were collected about weekly by removing two 100 cm^2 bark disks from each tree at each of two sample heights, 0-1 m and the central meter of infested bole (2-3 m above ground level for LMP at White Pine Coulee and 3-4 m for LMP at Jim Creek and LPP at both sites). Cumulated egg gallery length, number of live and dead brood of each instar and apparent cause of mortality of each cadaver was recorded for each disk.

All dead individuals in samples taken after winter could not be accurately counted due to their decay. The relationship between number of eggs per gallery and egg gallery length was determined by linear regression separately for hosts and sites, using data collected before winter. The appropriate regression equation was used to estimate the expected number of eggs per gallery

from egg gallery lengths measured in both host species in the field.

Development of *D. ponderosae* was described and compared among hosts using a development index. Instars were assigned the values one to seven for eggs, first, second, third, fourth larval instars, pupae, and adults, respectively. The development index was calculated as the average instar in the samples.

Instar-specific mortality was estimated using only samples in which all live individuals were of instars later than the one under consideration. It was calculated for each instar as the ratio of the total number of individuals that died in that instar, summed over all the samples involved, to the total number of individuals (live and dead) of that instar and later instars present in the samples. Total mortality from egg to adult was calculated by multiplying each instar-specific mortality value by the proportion of the original number of individuals that lived to reach that instar and summing for all instars.

Causes of death were assigned to dead insects as follows: resinosis (entrapment and death by resin)- cadavers covered in resin and without other injuries; parasitism- cadavers with parasitic larvae or paralyzed with parasitoid eggs; predation- abandoned, partially

devoured cadavers or cadavers on which insect predators were feeding; cold- larvae not bloated but contracted longitudinally and dark brown to black; and unknown.

Statistical analysis. The MINITAB statistical package (Ryan *et al*. 1985) was used for all analyses of variance, regressions and χ^2 tests.

C. Results

Emergence and host attack. Emergence and attack periods of MPB populations in LMP overlap considerably with those in LPP at both sites (Fig. IV-1). In 1985, LPP beetles emerged seven days before LMP beetles at White Pine Coulee and LPP were attacked by beetles 7-8 days earlier than LMP at both sites. Male: female ratios among beetles that emerged from LPP and LMP were similar at 0.47 (n = 28) and 0.62 (n = 136), respectively (χ^2 = 0.37, df = 1, P = 0.95). In 1986, beetles started to emerge from LMP on 2 July and from LPP on 12 July. Attack densities on LMP and LPP boles below 2.5 m (1.8 ± 1.38 (SD) and 2.1 ± 1.52 per 100 cm², respectively) were not significantly different (F = 1.47, df = 1, 130, P = 0.23). However, attack densities above 2.5 m were significantly higher (F = 4.84, df = 1, 100, P < 0.05) on LMP (1.0 ± 1.00 per 100 cm²) than on LPP (0.6 ± 0.93). Attack patterns on both tree species were similar with the bole between 1.5 and 2.5 m attacked first followed by

the lower and upper sections. On average, about 1/3 of the length of LPP boles was attacked whereas over 2/3 of the length of LMP boles was attacked.

There was no re-emergence of *D. ponderosae* from either host species. Most parents died in the galleries after completion of oviposition but a small proportion (< 10%) were still alive on 20 September. It is not known how many of these survived winter and reproduced the following year.

Fecundity. The number of eggs per cm of gallery length (Table IV-1) was significantly higher for *D. ponderosae* populations in LMP at both localities (Table IV-1). The equations describing regression of number of eggs per sample on accumulated gallery length per sample (Table IV-1) were considered satisfactory for estimating brood size from gallery lengths measured in the field because R^2 values were high. The length of MPB galleries in LMP did not differ significantly from those in LPP in either locality (Table IV-1). However, average number of eggs per gallery and brood density in LMP was significantly higher than in LPP at both White Pine Coulee and Jim Creek (Table IV-1). Beetles infesting LMP at Jim Creek produced a higher number of eggs per cm ($F = 8.93$, $df = 1, 54$, $P < 0.01$), number of eggs per gallery ($F = 12.86$, $df = 1, 75$, $P < 0.01$) and brood density ($F = 5.38$, $df = 1, 80$, $P < 0.05$) than beetles infesting LMP at

White Pine Coulee, but there was no difference in gallery length ($F = 2.94$, $df = 1, 75$, $P = 0.10$). There was no significant difference in all four parameters between localities for beetles infesting LPP.

Development. Development of *D. ponderosae* followed a similar pattern at both localities (Table IV-2). The development index of brood in LMP was less than that in LPP at first. However, by 20 September brood development in LMP was ahead of that in LPP. Due to the accelerated development of *D. ponderosae* populations in LMP at Jim Creek, beetles overwintered in a 15:69:16 ratio (development index = 3.00) of first: second: third instar larvae, whereas the corresponding ratio in LPP was 32:68:0 (development index = 2.68) ($\chi^2 = 22.2$, $df = 2$, $p < 0.001$). Similarly at White Pine Coulee beetles overwintered in a 40:60 ratio of first:second instar larvae (development index = 2.61) in LMP and 73:27 (development index = 2.27) in LPP ($\chi^2 = 22.2$, $df = 1$, $p < 0.001$)

The increase in development index between pre-winter (20 September) and post-winter (4 June) sample dates indicates some development between those dates, most of which likely occurred in May. Also, the greater mortality of smaller larvae over the winter may be partly responsible for the increase in development index.

Mortality. Instar-specific mortality was highest in the second larval instar (Table IV-3). Total mortality from egg to adult ranged from 87% to 100%. The most important mortality agent affecting the first three larval instars of *D. ponderosae* populations overall was winter-kill. However, overwintering mortality was lower among *D. ponderosae* populations in LMP than in LPP. Resinosis was the primary cause of mortality among eggs in all populations and also was responsible for death of many first instar larvae. Mortality due to resinosis was higher in LMP at both sites.

Predators and parasitoids caused mortality among all instars but were the primary causes of mortality among fourth instar larvae and pupae. Predatory species included a dolichopodid fly larva, *Medetera aldrichii* Wheeler; a clerid beetle, *Thanasimus undatulus* (Say); a tenebrionid beetle, *Corticeus praetermissus* (Fall); a rhizophagid beetle, *Rhizophagus dimidiatus* Mannerheim; and the staphylinid beetles, *Placusa* sp., *Quedius laevigatus* Gyllenhal and *Nudobius cephalus* Say. Another tenebrionid, *Corticeus subopacus* (Wallis), preyed on *D. ponderosae* in LPP but was uncommon and was not found in LMP. The major parasitoid utilizing *D. ponderosae* in both host trees was the braconid wasp, *Coeloides rufovariegatus* (Provancher).

D. Discussion.

Some of the main selective pressures acting on phytophagous insects likely stem from the morphological, biological, and especially chemical characteristics of the host plants (Strong *et al*. 1984). Although the chemical composition of LMP (a soft pine) phloem has not been studied and, therefore, cannot be compared to that of the well studied LPP (a hard pine), the two species likely differ greatly. Other soft pine species do differ markedly in phloem chemistry from that of hard pines (Mirov 1961). Chemical and physical differences between LPP and LMP may well explain some of the differences in phenology, fecundity, development, and mortality among *D. ponderosae* populations inhabiting the two species.

Phloem thickness limits the portion of the bole that is utilized and influences *D. ponderosae* fecundity, develoment and survival (Safranyik and Jahren 1970; Amman and Cole 1983). A greater proportion of the bole of LMP is utilized for *D. ponderosae* reproduction than that of LPP. Also, a higher number of eggs per cm of egg gallery and total number of eggs per gallery (fecundity) is produced in LMP than in LPP (Table IV-1). These differences may be explained by differences in phloem thickness, and thus food supply, between the two hosts. Although no measures of phloem thickness were made, the phloem of LMP is clearly thicker than that of LPP of

similar diameter in Alberta. Also, controlled breeding studies, in which phloem thickness of bolts was controlled, indicate that LMP phloem may be of better nutritional quality (Chapter III). Similarly, the faster brood development in LMP (Table IV-2) may be explained by greater quantity or quality of phloem or differences in temperature. The LMP stands studied were much more open and sun-exposed than the dense, shaded stands of LPP. Greater exposure of boles to the sun results in higher subcortical temperatures (Powell 1967) which can accelerate development.

Instar-specific mortality was generally highest in the second larval instar (Table IV-3), mainly because that was the principal overwintering instar and was subjected to high overwintering mortality. The major source of mortality for *D. ponderosae* in both hosts and both localities was winter-kill but was much lower among populations in LMP than in LPP. This may, in part, be related to the greater development of brood in LMP than in LPP at the start of the winter (Table IV-2). Amman (1973) found that larger larvae of *D. ponderosae* were more cold-hardy than small larvae. This difference in cold tolerance among larval instars is difficult to explain because Sômme (1964) demonstrated no difference in glycerol content among the first three larval instars of *D. ponderosae*; the fourth larval instar was not

examined. In this study, beetles in LMP may have been afforded greater insulation from cold by thicker phloem and/or higher subcortical temperatures due to the greater sun-exposure of LMP.

Total mortality measures (Table IV-3) are believed to be underestimates, especially for populations at Jim Creek, mainly because dead eggs are easily overlooked and both eggs and small larvae may be entirely ingested by predators.

Although it is true that LPP and LMP present two markedly different selective environments for *D. ponderosae*, clearly affecting fecundity, development and mortality, there is no apparent separation of the life histories of beetle populations among hosts. Thus, there is no phenological barrier which may contribute to genetic divergence of the two *D. ponderosae* populations.

Since *D. ponderosae* broods develop faster in LMP than in LPP in the field (Table IV-2) and in the laboratory (Chapter III), one might expect beetles in LMP to emerge and attack new hosts earlier than those in LPP. Although this was not the case in 1985 (Fig. IV-1), beetles did start to emerge from LMP about two weeks earlier than from LPP in 1984 (Smith 1984) and about ten days earlier in 1986. If there was strong host fidelity, one might expect the emergence/ host attack periods of

beetles reared in LMP and LPP to diverge with each successive generation, thus leading to a phenological barrier to gene flow between the two populations, such as occurs for host races of *Rhagoletis* (Bush 1969), *Laspeyresia pomonella* (L.) (Phillips and Barnes 1975), *Alsophila pometaria* (Harris) (Mitter *et al.* 1979) and *Enchenopa binotata* Say (Wood 1980). However, host fidelity among *D. ponderosae* populations in LMP and LPP in Alberta appears unlikely (Chapter II).

Population genetics studies indicate significant genetic divergence at three loci in co-occurring populations of *D. ponderosae* in LMP and LPP at White Pine Coulee but no divergence between populations in different hosts at Jim Creek (Chapter II). The genetic divergence of beetles in different hosts at White Pine Coulee could be explained by differential selection pressures in the two host species just as well as by preferential selection of hosts (host fidelity). Host switching and inter-breeding between beetles in different tree species, which likely occurs commonly during the epidemic and declining phases of the *D. ponderosae* population cycle (Richmond 1933; Wood 1982), may explain the lack of any significant temporal separation of life histories of beetles in the two hosts in 1985 and 1986. During the endemic phase when host fidelity is believed to be stronger (Baker *et al.* 1971; Wood 1982), there may be

greater temporal separation of the life history of *D. ponderosae* in the two hosts. A study of the life history of endemic *D. ponderosae* populations in different host species may provide some insights into scolytid speciation.

These studies indicate that LMP is more suitable for *D. ponderosae* fecundity, development and survival than is LPP. This suggests that *D. ponderosae* populations in LMP have the potential to increase much faster than in LPP and may serve as epicenters for future beetle epidemics. Controlled breeding studies indicate that *D. ponderosae* reared from LMP and LPP are compatible with either host (Chapter III). Hence, residual beetle populations in the commercially unimportant and, therefore, sometimes ignored LMP are vital because there is no apparent barrier that will prevent the beetles from reinvading, under appropriate conditions, the more valuable LPP stands. This possibility argues for regular surveillance and appropriate treatment of *D. ponderosae* populations in LMP and other commercially unimportant tree species.

Table IV-1. Mean number of eggs per cm gallery length, gallery length, eggs per gallery and brood density for mountain pine beetle field populations in lodgepole pine (LPP) and limber pine (LMP) at two localities in southwestern Alberta in 1985. E- eggs, GL- egg gallery length.

Parameter	White Pine Coulee		Jim Creek	
	LPP	LMP	LPP	LMP
Eggs/cm gallery length				
no. 100 cm² samples	39	16	41	40
mean ± SD	1.3 ± 0.30	1.5 ± 0.43	1.3 ± 0.29	1.8 ± 0.34
F-ratio & signif.	F = 5.94, p < 0.05		F = 52.25, p < 0.001	
regress. equation	E=0.92 + 1.23GL	E=1.03 + 1.65GL	E=0.19 + 1.34GL	E=1.18 + 1.72GL
R^2	0.84	0.73	0.87	o.83
Gallery length (cm)				
no. galleries	47	43	31	34
mean ± SD	27.8 ± 8.53	26.4 ± 9.21	27.4 ± 7.77	29.5 ± 9.90
F-ratio & signif.	F = 1.37, n.s.		F = 1.58, n.s.	

Table IV-1 cont'd.

Eggs/gallery'				
no. galleries	47	43	31	34
mean ± SD	35.2 ± 10.49	41.3 ± 15.22	36.9 ± 10.51	54.5 ± 17.05
F-ratio & signif.	F = 5.02, p< 0.05		F = 24.43, p < 0.001	
Brood density (per 100 cm²)				
no. 100 cm² samples	31	40	38	42
mean ± SD	19.0 ± 10.64	25.4 ± 12.10	21.9 ± 11.23	31.8 ± 13.03
F-ratio & signif.	F = 8.74, p < 0.01		F = 11.63, p < 0.01	

' estimated by substituting the length of each gallery measured in the field into the appropriate regression equation.

Table IV-2. Mean development (SD) index of *D. ponderosae* in lodgepole pine (LPP) and limber pine (LMP) at two localities in southwestern Alberta for various sampling dates in 1985 and 1986.

Date	White Pine Coulee			Jim Creek		
	LPP	LMP	F	LPP	LMP	F
28 July 1985	1.00 (0.00)	0	-	1.00 (0.00)	0	-
6 Aug. "	1.00 (0.00)	1.00 (0.00)	-	1.00 (0.00)	1.00 (0.00)	-
14 Aug. "	1.03 (0.01)	1.00 (0.00)	0.0	1.07 (0.25)	1.10 (0.30)	0.3
23 Aug. "	1.19 (0.40)	1.20 (0.38)	0.0	1.25 (0.43)	1.74 (0.45)	95.2***
31 Aug. "	1.49 (0.54)	1.60 (0.61)	0.1	1.61 (0.63)	2.32 (0.76)	99.6***
20 Sept. "	2.27 (0.75)	2.61 (0.78)	4.5*	2.68 (0.80)	3.00 (0.91)	9.7**
4 June 1986	-[1]	3.50[2] (1.53)	-	4.00[2] (0.00)	4.31 (0.54)	1.3
18 June "	-	5.00[2] (0.00)	-	5.00[2] (0.00)	6.16 (0.71)	17.5***
26 June "	-	6.50[2] (0.58)	-	6.00 (0.00)	6.69[2] (0.54)	3.1
2 July "	-	7.00[2] (0.00)	-	7.00[2] (0.00)	6.96 (0.19)	0.1

[1] no beetles survived winter.

[2] estimate is based on 6 or less specimens; other estimates were based on > 25 specimens.

statistical tests were significant at the 95% (*), 99% (**), or 99.9% (***) level

Table IV-3. Instar-specific mortality, total mortality from egg to adult and percent mortality due to each causal agent for mountain pine beetle populations in lodgepole pine (LPP) and limber pine (LMP) at two localities in southwestern Alberta in 1985 and 1986.

Parameter	White Pine Coulee		Jim Creek	
	LPP	LMP	LPP	LMP
Instar-specific mortality (%)				
eggs	22.9 (33.7)[1]	7.5 (0.0)	14.8 (6.6)	14.0 (6.4)
larvae I	63.5 (20.9)	31.1 (9.0)	28.5 (17.9)	19.1 (6.2)
larvae II	80.3 (5.5)	84.1 (22.3)	78.0 (31.2)	58.5 (28.9)
larvae III	100.0[2] (0.0)	63.2 (46.9)	48.1 (21.8)	46.5 (23.7)
larvae IV	-	16.7[3] (19.2)	30.0 (42.7)	11.7 (12.2)
pupae	-	0.0[3] (0.0)	0.0[3] (0.0)	4.9 (57.2)
Total mortality (%)	100.0	97.0	95.1	87.0
Mortality due to each causal agent				
resinosis	13.0	18.6	9.1	17.3
predators	6.4	9.6	6.2	9.7
parasitoids	2.5	6.1	4.6	2.5
cold	52.4	46.1	48.1	34.8
unknown causes	25.7	16.6	27.1	22.7
Total	**100.0**	**97.0**	**95.1**	**87.0**

Table IV-3 cont'd

[1] numbers in parentheses are standard deviations

[2] no beetles survived winter

[3] estimate based on a small sample size; other estimates based on > 25 specimens

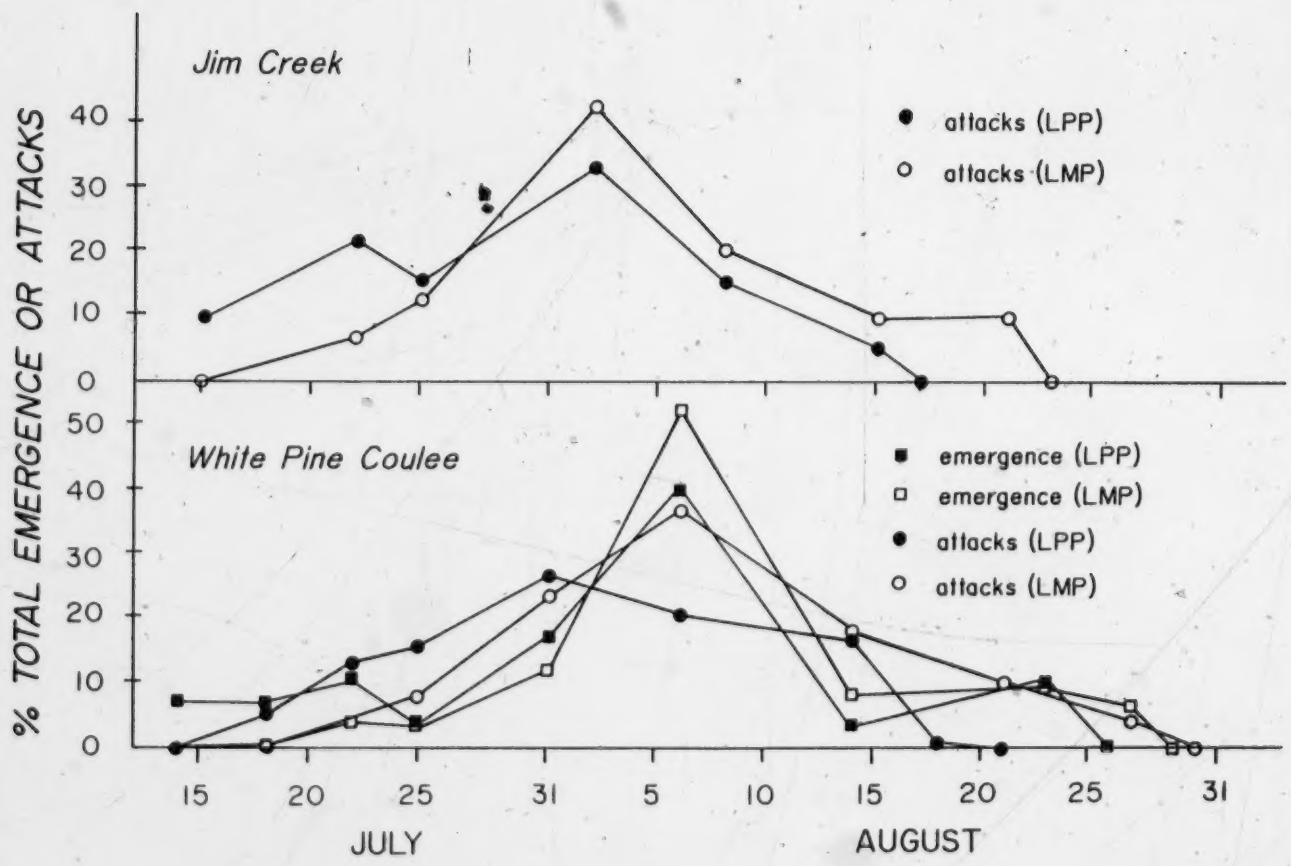

Fig. IV-1. Emergence and host attack periods of the mountain pine beetle in lodgepole pine (LPP) and limber pine (LMP) at two localities in southwestern Alberta in 1985.

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V. GENERAL DISCUSSION

There is no doubt that LPP and LMP present markedly different selective environments to *D. ponderosae* populations utilizing them for food and reproduction. Although the chemical composition of LMP (a soft pine) has nct been determined, and therefore cannot be compared to that of LPP (a hard pine), other soft pine species generally differ greatly from hard pines (Mirov 1961). The two species also differ physically in terms of growth form and more importantly, as far as *D. ponderosae* is concerned, phloem thickness; phloem of LMP appears to be generally thicker along the entire length of the bole than that of LPP of similar dimensions (Chapter IV). Also, LMP tends to grow on or near ridge tops and in open stands so that the boles are more sun-exposed than are boles of LPP, which generally grow in more dense stands. This likely results in generally higher subcortical temperatures in LMP.

Regardless of the relative contribution of the above factors (and others) to the selective pressures exerted by LPP and LMP on MPB populations, together they are responsible for host effects on the genetics, morphology and biology of *D. ponderosae*. Study of population dynamics in the field (Chapter IV) indicated that MPB infesting LMP had significantly higher fecundity, produced more eggs per cm of gallery length (Table IV-1)

and their progeny developed faster (Table IV-2) and survived better (Table IV-3) than beetles infesting LPP. Similarly, controlled breeding studies (Chapter III) indicate that beetles introduced into LMP produced shorter egg galleries and more eggs per cm of gallery length (Table III-3) and their progeny generally experienced faster development and lower mortality (Table III-4) than beetles introduced into LPP. Both of these studies suggest that LMP is a better host for mountain pine beetle reproduction, development and survival than LPP. This agrees with studies by Amman (1982) which also indicated that soft pine species were better hosts than hard pine species. Also, analysis of genetic and morphological variation in *D. ponderosae* populations (Chapter II) revealed significant host effects on allozyme variation at three polymorphic loci (Table II-9) and on beetle shape (Table II-13).

Differential host-generated selection pressures have important implications for insect population divergence and host race formation (Diehl and Bush 1984). In order for the diversifying effects of natural selection (and genetic drift) to generate significant genetic divergence of *D. ponderosae* populations in LPP and LMP, it is necessary to restrict gene flow between populations (Futuyma and Peterson 1985). Population genetics models indicate that an exchange of only one individual per

generation between two populations may be enough to keep them from diverging by genetic drift (Slatkin 1987).

A necessary prerequisite for population divergence, host race formation and sympatric speciation is strict host fidelity (Kondrashov and Mina 1986). Although there is host-associated allozyme and morphological variation within declining *D. ponderosae* populations in Alberta, there is little evidence of preferential host selection by beetles which would imply sub-structuring of populations along host lines. However, due to circumstances beyond control, the experimental protocol used to sample beetles was not the most conducive to evaluate host fidelity. Sampled beetles were collected from host trees before emergence. Thus, the observed differences in allozyme frequencies among beetles from lodgepole pine and limber pine may have been a result of host fidelity or simply the differential selection pressures exerted by the hosts via juvenile mortality. Ideally, beetles should have been collected from hosts during colonization in addition to those collected before emergence.

Although analysis of allozyme variation of beetles colonizing hosts can reveal whether mating among beetles from different hosts is random or assortive, it tells little about strictness of host preference. To obtain this objective it is necessary to determine the host

origin of each beetle colonizing a tree. In the past researchers have experimented with marking bark beetles with radioactive tags (Schmidt 1970; Moore and Taylor 1976; Taylor and Moore 1978) and fluorescent powders (Linton *et al.* 1987) for studies of dispersal. However, such marking procedures can be effective in host fidelity or host switching studies only if all bark beetles from one host in an area are marked and if immigration into the area is prevented, and this is virtually impossible. However, the recent development of a technique of measuring chromatin distribution in cells of insects (Peet and Sahota 1984; Sahota *et al.* 1986) may have great use in host fidelity/switching studies. Using this technique researchers have distinguished (with very high probability) among scolytids reared under different population densities (Sahota *et al.* 1987) and among beetles reared in different regions, which differed in phloem thickness, of the same tree (Sahota *et al.* 1984). One might also expect great differences among beetles from different host species, and this possibility is currently being investigated.

Although it is the female that selects and initially colonizes the host (Amman and Cole 1983), males must also exhibit strict host fidelity to allow population divergence. Since males respond to female-produced pheromones and host volatiles, population divergence

along host lines requires that pheromones produced by females be functionally different. Pheromone differences have been reported for *D. ponderosae* infesting different host species (McKnight 1979) but more detailed studies should be made on type and relative abundance and quality of attractants produced in diferent hosts, synergists and chirality of pheromones (Lanier and Burkholder 1974; Birch *et al.* 1980).

Allochronic separation of emergence and host attack times among beetle populations from different host species may also restrict gene flow between them and reinforce the consolidation of host-adapted genes. Although there was a host effect on time of emergence and host attack there was enough overlap to allow interbreeding of populations (Fig. III-1). If there was sufficient host fidelity one might expect the emergence and host attack periods of beetles reared in the two hosts to diverge with each successive generation, thus leading to a phenological barrier to gene flow between the two populations. This has been reported for several other insects (Bush 1969; Phillips and Barnes 1975; Mitter *et al.* 1979; Wood 1980).

Finally, some behavioural, morphological or physiological incompatibility between beetles from different hosts during courtship and mating may further restrict gene flow between populations. All crosses of *D.*

ponderosae from LPP and LPP produced fertile offspring (Table III-6), although there were some host effects on reproductive success (Table III-2), fecundity (Table III-3), development (Table III-4), and mortality (Table III-4). However, in these studies males were forced into galleries with females and prevented from leaving by blocking the entrance with gelatin capsules. This may have disrupted normal courtship behaviour. To adequately determine if there is some courtship-based pre-mating reproductive isolation, courtship and mate selection must be allowed to proceed normally.

Richmond (1933) and Wood (1982) contend that under epidemic conditions many or all acceptable host species may be attacked by *D. ponderosae* in a given region and host switching occurs. Host preference by *D. ponderosae* appears to be more clearly expressed during endemic population levels (Evenden *et al.* 1943; Baker *et al.* 1971). Thus, if endemic situations persisted for long periods genetic divergence of sympatric populations might occur (Bush 1975).

There has been little or no work done with endemic *D. ponderosae* populations in the past mainly because of the difficulty in finding beetles. However, with the identification, production and testing of *D. ponderosae* pheromones in recent years (Pitman and Vite 1969; Conn *et al.* 1983; Cerezke *et al.* 1984), we now have a tool to

locate endemic mountain pine beetle populations for study. Studies of host preference and genetic differentiation of endemic *D. ponderosae* populations as well as a repitition of the controlled breeding studies using endemic populations from different host species may provide some insights into speciation of the Scolytidae and are well worth pursuing.

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